How Do Mammals Buffer Environmental Seasonality? The Role of Brain Size, Body Fat and Allomaternal Care in Dealing with Energy Shortage

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von

Sandra Andrea Heldstab

von

Saas GR

Promotionskommission

Prof. Dr. Carel van Schaik (Vorsitz)

PD Dr. Karin Isler (Leitung der Dissertation)

Prof. Dr. med. vet. Marcus Clauss

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“There is a time for everything,

and a season for every activity under the heavens…”

(Ecclesiastes 3)

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Summary

Humans stand out among mammals in having a unique combination of three traits, a large brain, hefty body fat stores and extensive allomaternal care. All three characteristics have been proposed to play a key role during hominin evolution in strategies to cope with seasonal food fluctuations. To obtain a better insight whether one or several of these three strategies indeed permitted our ancestors to buffer seasonality, we investigated how other mammalian species, including our closest relative, the primates, deal with seasonal food scarcity. Thus, the main topic of this thesis is to examine in a phylogenetic comparative approach across a large sample of over 100 mammalian species (i) which strategies different species use to buffer environmental seasonality, (ii) under which ecological conditions a particular strategy is more likely to occur, and (iii) how these different buffering strategies are connected to each other.

The aim of chapter 2 was to investigate whether large brains confer an enhanced ability to survive in seasonal habitats (cognitive buffering). Using a new method to classify the complexity of food manipulations across primate species, we showed that complex manipulative skills are consistently positively correlated with brain size and cognitive test performance. Due to this positive relationship with brain size, and because enhanced manipulative skills provide access to hidden food sources of high nutritive content during periods when other food sources are scarce, we conclude that they can be seen as a very energetically rewarding cognitive buffer strategy. We further found that terrestriality had a positive effect on the relationship between manipulation complexity and brain size. Overall, this pattern suggests that a terrestrial bipedal lifestyle in combination with high intelligence may have allowed for cognitive buffering in the hominin lineage through tool use and other advanced food processing technologies far beyond the range of other, more arboreal primates.

In chapter 3, we used seasonal variation in body mass as a proxy to assess a physiological buffering strategy of fat storage. Using coefficients of variation (CV) of body mass data obtained from the literature, we found a negative correlation between the ability to store body fat and relative brain size in the subsample of arboreal mammals, indicating that cognitive and physiological buffering are compensatory strategies to buffer food shortages. In contrast, in predominantly terrestrial species, this correlation was not significant, suggesting that the reduced cost of transporting additional body fat alleviates this trade-off and thus allows organisms to combine both buffering strategies. These results help to explain how humans managed to combine both strategies on how to solve the energetic challenge that seasonality poses: When our ancestors adopted habitual terrestrial (bipedal) locomotion, this lowered the costs of transport for additional adipose tissue, allowing for the combination of physiological buffering through

storing large amounts of body fat and cognitive buffering by having the relatively largest brain of all land-living mammal.

In chapter 4, we proposed a new buffering strategy, "care buffering", in which reproductive females are hypothesized to buffer seasonality by receiving allomaternal care, which distributes the costs of reproduction over several individuals. We predicted that these breeding females store less body fat themselves if fathers or other non-breeding group-members help to cover the energetic demands for offspring production. Breeding females benefit from storing smaller amounts of body fat, as large adipose depots lead to fitness costs such as higher predation risk or decreased hunting success. Consistent with the existence of a care buffering strategy, we found that reproductive females in those mammalian species with high amounts of allomaternal care exhibit reduced annual variation in body mass as a proxy for the tendency to store body fat. These results show that both storing fat and allomaternal energy subsidies independently stabilise the energetic costs for female reproduction in seasonal habitats. Humans are also unique for a land-living mammal in this respect by combining large body fat stores and high levels of allomaternal infant care to buffer against resource uncertainty.

Overall, the most important contribution of this thesis is to show that the hominin lineage was able to buffer seasonality with strategies that individually also allow other animal lineages to cope with seasonal food fluctuations, but in combination are unique for our species. Furthermore, the results of this thesis highlight the key role of a terrestrial lifestyle with efficient bipedal walking in making this unique combination of all three buffer strategies possible. Thus, bipedal terrestriality allowed our ancestors to thrive in increasingly seasonal habitats.

Zusammenfassung

Uns Menschen zeichnet eine einzigartige Kombination von drei Merkmalen aus: Wir haben extrem grosse Gehirne für unser Körpergewicht, einen grossen Körperfettanteil und wir sorgen gemeinschaftlich für unseren Nachwuchs. Wissenschaftler vermuten, dass alle drei Merkmale eine Schlüsselrolle in der menschlichen Evolution spielten, um saisonale Nahrungsknappheit zu bewältigen. Um zu untersuchen, ob diese drei Strategien unseren Vorfahren tatsächlich halfen, Nahrungsfluktuationen zu überleben, liegt der Fokus meiner Dissertation darauf, wie Säugetierarten und Primaten, unsere nächsten Verwandten, dieses Problem lösen. Mittels eines phylogenetischen vergleichenden Ansatzes über mehr als 100 Säugetierarten untersuchte ich (i) welche Strategien verschiedene Arten benützen, um Zeiten des Nahrungsmangels zu überbrücken, (ii) welche Lebensweisen und Umwelten bestimmte Strategien begünstigen, und (iii) wie diese verschiedenen Strategien miteinander verknüpft sind. Vor diesem Hintergrund ist die vorliegende Dissertation in drei Teile gegliedert:

Anschliessend an eine Einleitung im ersten Kapitel untersuchte ich im zweiten Kapitel, ob ein grösseres Gehirn relativ zum Körpergewicht und die damit einhergehenden gesteigerten kognitiven Fähigkeiten beim Überleben in saisonalen Habitaten helfen («cognitive buffering»). Hierfür benutzten wir eine neu entwickelte Methode, um die Komplexität der Arm-, Hand- und Fingerfertigkeiten in 37 verschiedenen Primatenarten bei der Nahrungsaufnahme zu klassifizieren. Mithilfe dieser Klassifizierung konnten wir aufzeigen, dass die relative Hirngrösse und die damit verbundene Intelligenz positiv mit der Komplexität der Futtermanipulation korreliert. Diese positive Korrelation, sowie die Annahme, dass eine komplexere Arm-, Hand- und Fingerfertigkeit in Zeiten der Nahrungsknappheit besseren Zugang zu versteckten Nahrungsressourcen gewährt, lässt uns schlussfolgern, dass dies eine lohnenswerte «cognitive buffer»-Strategie ist. Des Weiteren konnten wir aufzeigen, dass bodenlebende Arten generell zu komplexeren Futtermanipulationen fähig sind als baumlebende Arten. Zusammengefasst weisen diese Resultate darauf hin, dass unsere Vorfahren saisonale Nahrungsknappheit so gut überstehen konnten, weil sie eine einzigartige Kombination von Merkmalen aufwiesen: eine hohe Intelligenz und einen terrestrisch zweibeinigen Gang.

Im dritten Kapitel benutzten wir jährliche Körpergewichtsschwankungen als Näherungsvariable für die Speicherung von Körperfett, eine Form des «physiological buffering». Die Daten für die Berechnung des Variationskoeffizienten des Körpergewichts erfasste ich aus 83 wissenschaftlichen Publikationen über ein weites Spektrum von 120 Säugetierarten. Mithilfe dieser Daten konnten wir zeigen, dass in arborealen Säugetierarten die Fähigkeit zur Fettspeicherung mit relativ kleineren Gehirnen einhergeht.

Die Erkenntnisse dieser Studie deuten darauf hin, dass «cognitive buffering» und «physiological buffering» kompensatorische Strategien sind, um saisonale Nahrungsfluktuationen zu überwinden. Im Gegensatz zu arborealen Säugetierarten war diese Korrelation zwischen Hirngrösse und der Fähigkeit zur Fettspeicherung in terrestrischen Arten nicht signifikant. Dies könnte darauf zurückzuführen sein, dass die Fortbewegung in bodenlebenden Arten nicht viel mehr Energie kostet, wenn diese etwas mehr Fettmasse speichern, und folglich der Trade-off zwischen Hirngrösse und der Fähigkeit zur Fettspeicherung in diesen Arten abgeschwächt ist. Vermutlich fällt das zusätzliche Körperfett auch beim aufrechten zweibeinigen Gang des Menschen energetisch weniger ins Gewicht. Dies könnte dazu geführt haben, dass sich Menschen im Laufe der Evolution schliesslich sowohl ein sehr grosses Gehirn als auch einen grossen Fettanteil leisten konnten. Demzufolge konnten Menschen beide Strategien («cognitive buffering» und «physiological buffering») nutzen, um Zeiten des Nahrungsmangels zu überstehen.

Im vierten Kapitel testeten wir die Hypothese, ob gemeinschaftliche Fürsorge bei der Jungenaufzucht den fortpflanzenden Weibchen in Zeiten saisonaler Nahrungsknappheit hilft («care buffering»). Dies erwarten wir, weil die zusätzliche Hilfe von anderen Gruppenmitgliedern bei der Jungenaufzucht die energetischen Kosten senkt, die das reproduktive Weibchen sonst alleine aufbringen müsste. In dieser Studie testeten wir folglich, ob Weibchen ihre Fähigkeit zur Fettspeicherung reduzieren, wenn sie Hilfe bei der Jungenaufzucht erhalten. Körperfett erlaubt es Weibchen, die hohen energetischen Kosten für die Trächtigkeit und Laktation zu decken. Körperfettmasse ist aber indirekt kostspielig: Grosse Mengen an Körperfett erhöhen den Räuberdruck, da ein fettes Individuum gegenüber seinen Artgenossen schwerfälliger und langsamer ist und daher eher erbeutet wird. Umgekehrt wird ein fettes schwerfälliges Tier einen tieferen Jagderfolg aufweisen als die schnelleren und wendigeren Individuen. Zudem muss Körperfett herumgetragen werden, was vor allem bei kletternden und fliegenden Tierarten einen grossen Energieaufwand bedeutet. Um den Zusammenhang zwischen der Fähigkeit zur Fettspeicherung der Weibchen und der Hilfe bei der Jungenaufzucht zu untersuchen, erfasste ich die jährliche Körpergewichtsvariation von 111 Säugetierarten als Proxy für die Fähigkeit zur Fettspeicherung. Unsere Resultate zeigen, dass Weibchen derjenigen Säugetierarten, welche Hilfe bei der Jungenaufzucht erhalten, weniger Energie in Form von Körperfett speichern. Eine Ausnahme der landlebenden Säugetiere ist dabei der Mensch, da wir Menschen diese beiden Strategien des «care buffering» und des «physiological buffering» kombinieren und somit gleichzeitig einen grossen Körperfettanteil wie auch eine ausgeprägte gemeinschaftliche Fürsorge für den Nachwuchs aufweisen.

Zusammenfassend zeigt diese Doktorarbeit, dass es unseren Vorfahren gelungen ist, saisonale Nahrungsfluktuationen mittels einer einzigartigen Kombination von Strategien, die einzeln auch in anderen Säugetierordnungen auftreten, zu überwinden. Des Weiteren unterstreichen die Resultate dieser Studien die Bedeutung einer terrestrischen Lebensweise mit einem energetisch effizienten zweibeinigen Gang, der diese besondere Kombination aller drei Strategien des «cognitive buffering», «physiological buffering» und des «care buffering» erst ermöglichte und es unseren Vorfahren erlaubte, neue, ausgesprochen saisonale Habitate zu besiedeln.

Chapter 1

General introduction

Humans have a unique combination of traits

Humans stand out among non-aquatic mammals by having an unusual combination of an extremely large brain (Striedter, 2005), relatively large adipose depots (Lawrence et al., 1987; Yamauchi et al., 2000; Sherry and Marlowe, 2007; Pontzer et al., 2012) and high levels of allomaternal care (Hrdy, 2009). Numerous hypotheses have been put forward to explain how this combination of human traits evolved. The critical issue is, however, how to test these evolutionary hypotheses, as such ultimate questions cannot be tested experimentally. The relationships examined are not directly causal but rather reflect a process of correlated evolution and thus show patterns across evolved equilibria. Moreover, selection experiments are usually restricted to short-living model organisms and can therefore not automatically be applied to test hypotheses concerning long-living mammals such as primates. As a consequence, a phylogenetically based comparative approach is key to understand the evolutionary history underlying present-day patterns. This approach also provides valuable information on evolutionary processes across many different species, which at the end also helps to explain how combinations of traits might have evolved. To understand the evolution of the unique human combination of a large brain, hefty body fat deposits and allomaternal care, we therefore need phylogenetically based comparative analyses covering a large number of mammalian species from different lineages.

Because in humans all these three traits have been suggested to buffer environmental seasonality (Kaplan et al., 2000; Wells and Stock, 2007; Wells, 2010; Smaldino et al., 2013), a broader insight into how other mammalian species cope with seasonal food scarcity is essential. The aim of this thesis is therefore to investigate three different buffering strategies of mammals and their relationship to brain size evolution. First, we took a closer look at a cognitive strategy, classifying food manipulations in primates (chapter 2). Second, we used seasonal variation in body mass as a proxy to assess a physiological buffering strategy of fat storage (chapter 3). Third, a new buffering strategy is proposed, "care buffering", in which the distribution of reproductive costs over a larger number of individuals is hypothesized to correlate with seasonality (chapter 4). All these hypotheses are tested in a comparative framework across mammalian species to examine under which ecological conditions a particular strategy is more likely to occur, and how these different buffer strategies are connected to each other.

What is seasonality?

Seasonality is the phenomenon of recurrent fluctuations in climatic conditions and environmental productivity over the year (Boyce, 1979; Lindstedt and Boyce, 1985). These fluctuations of environmental conditions are a basic consequence of the tilt of 23.5 degrees of the Earth's rotational axis relative to its orbital plane (Pianka, 2011). As a result, four specific points in Earth's trip around the sun serve as the astronomical definition of the seasons (Fig. 1): the two solstices and the two equinoxes.

The summer solstice in the northern hemisphere occurs around June 21, when Earth's axis is closest to the sun. At this time, the amount of sunlight reaching the northern hemisphere is at a maximum and therefore it is the longest day of the year. In the southern hemisphere, the same day is the winter solstice and the shortest day of the year, when the Earth's axis is farthest from the sun, leading to a minimum of sunlight reaching the southern hemisphere. Around December 21, the winter solstice occurs for the northern hemisphere and the summer solstice for the southern hemisphere. In both hemispheres, the summer solstice is considered the first day of summer according to the astronomical definition of the seasons, while the winter solstice marks the first day of astronomical winter.

The other two significant days during the journey of the Earth around the sun are the equinoxes. On these days, the Earth's axis is pointed parallel to the sun, rather than tilted toward or away from it, meaning that day and night are of approximately equal duration all over the planet. The astronomical spring, or vernal equinox for the northern hemisphere takes place around March 20. At the same day on the southern hemisphere autumnal equinox occurs marking the beginning of astronomical autumn. The vernal equinox ushers in the first day of astronomical spring in the southern hemisphere around September 22, while this day marks the first day of astronomical autumn in the northern hemisphere (autumnal equinox).

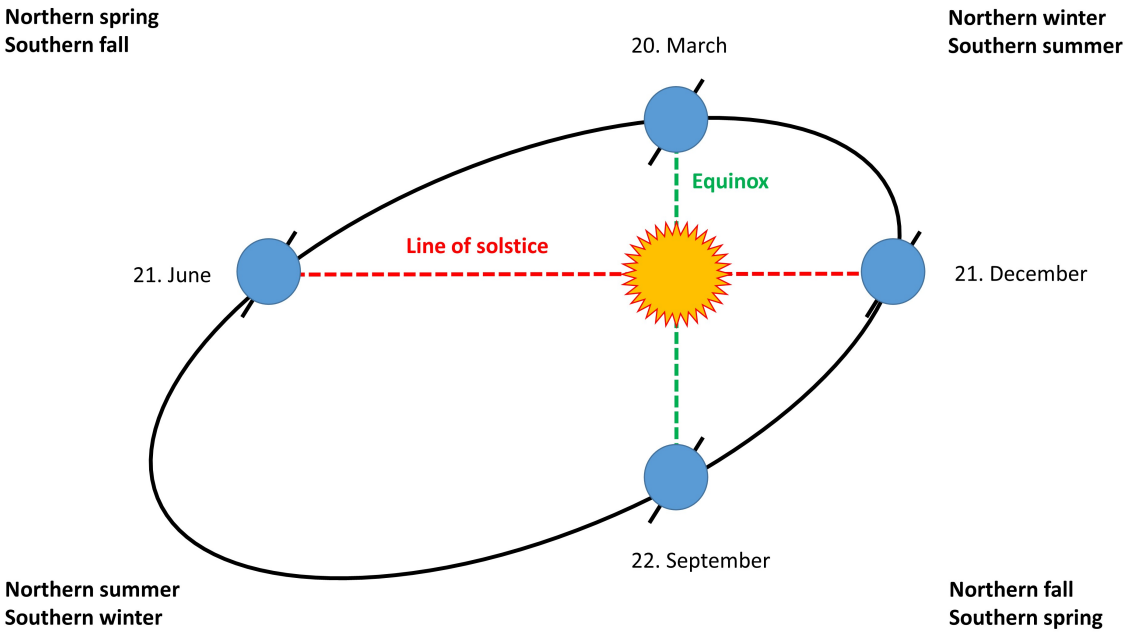

Figure 1. Seasons are caused by the Earth's axial tilt (modified from Lianko, 2001).

The Earth's axial tilt is also responsible for the difference in intensity and duration of sunlight received by different locations on the Earth. This is the case because as the Earth orbits the sun, the relative position of the Earth's axis to the sun changes during the cycle which causes one hemisphere and then the other to receive more direct sunlight resulting in longer day light. Therefore, solar radiation varies considerably throughout the year from season to season at polar latitudes and is relatively stable at tropical latitudes (Fig.2).

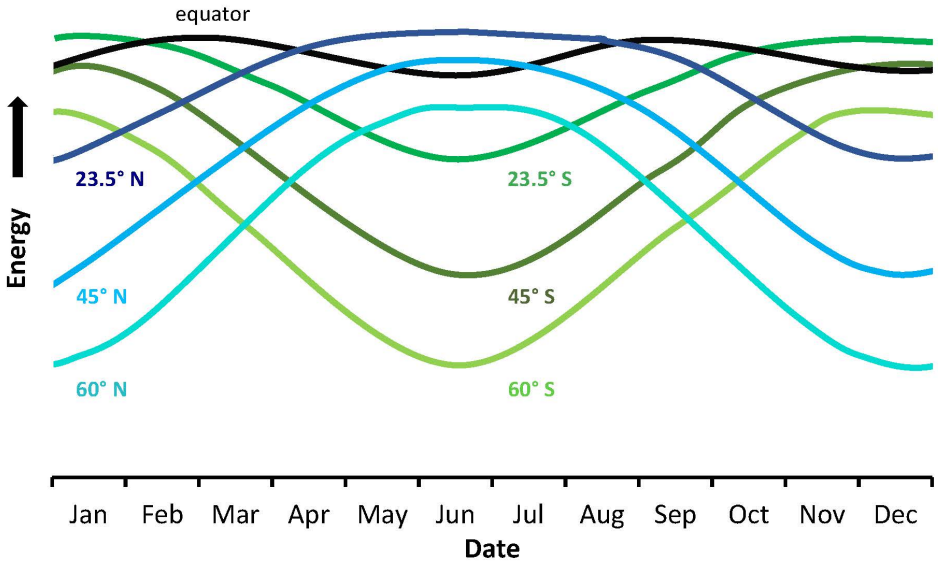

Figure 2. The solar radiation received at local noon each day of the year depends on the latitude. At the equator in the tropics (black line), the amount of solar radiation changes very little throughout the year. However, at high northern (blue lines) and southern (green) latitudes, there is a considerable seasonal change in solar radiation. (modified from http://earthobservatory.nasa.gov/Features/EnergyBalance/page3.php).

Impact of seasonality on mammals

As the sun affects not only sunshine and temperature but also other aspects of climate, such as windiness, sea temperature and rainfall (e.g., Trenberth, 1997; Trenberth et al., 2000), seasonality is felt by mammals all around the globe, even in the tropics. The impact of climate on mammals can be direct or indirect. Direct responses to changing weather conditions comprise behaviours such as seeking shelter to avoid rain (Snoeks et al., 2015), windchill (Staines, 1976), direct sunlight (Staines, 1976), or cold temperatures (Schmid and Kappeler, 1998), changing body posture (Dasilva, 1993) or changing the degree of sociality, e.g. during resting periods (Morland, 1993; Perret, 1998; Pereira et al., 1999), to reduce heat loss due to a reduction of the exposed surface. However, the major impact of climate on mammals is indirect through the effects of climate on primary productivity and thus nature and distribution of potential food items, both plants or animals.

Already Charles Darwin (1859) identified that food is a key limiting resource for almost every animal, at least during certain seasons. On the proximate level, food scarcity imposes severe energetic constraints which lead in the first place to weight loss (Goldizen et al., 1988) and a reduction in body fat (Knott, 1998;

Pond, 1998; Schmid, 1999; Pond, 2011). If the period of low food availability is prolonged, this can severely impact fecundity (Wade and Schneider, 1992; Gill and Rissman, 1997; Cowlishaw and Dunbar, 2000; Temple et al., 2002; Kauffman et al., 2010), growth (Derting, 1989; Boutin and Larsen, 1993) and lastly also survival (Hamilton, 1985; Gould et al., 1999). Therefore, it is really essential for an individual to cover its minimal energetic needs to maintain a positive energy balance in the long term. If food availability drops below the minimal energetic need due to environmental seasonality, the subject falls into a period of negative energy balance that needs to be dealt with (blue zone in Fig. 3a). There are two possible and complementary ways how this can be done. The first possibility is to decrease the minimal energetic need to the lowest point in the lean period (Fig. 3b). The second way is to buffer the environmental seasonality by keeping the net energy intake more constant throughout the year (Fig. 3c).

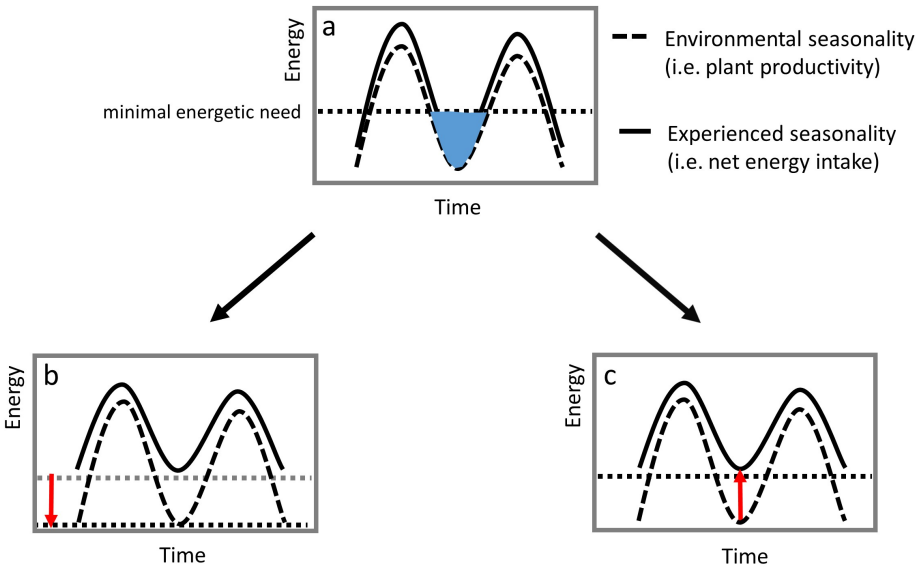

Figure 3. The consequences of living in a seasonal habitat on energy intake (modified from van Woerden et al., 2010; van Woerden, 2011). If the environmental seasonality and hence food resources drop bellow the minimal energetic need (blue area **a**), subjects can either decrease minimal energetic need (**b**) or buffer seasonally lean periods by keeping energy intake throughout the year more constant (**c**).

How do mammals cope with seasonal food scarcity?

As mentioned above, food scarcity can have severe fitness consequences for individuals. Therefore, natural selection favours changes in physiology and behaviour that on average yield a better adaptation to these seasonal food fluctuations (Winterhalder and Smith, 2000). Mammals have evolved various strategies how to solve this problem of seasonal food scarcity to achieve either a more constant energy intake (cognitive buffering, active strategy of survival) or a decrease in minimal energetic need (physiological buffering, passive strategy of survival).

Cognitive buffering

While physiological buffering aims at reducing energy expenditure during lean periods, cognitive buffering yields a stabilization of energy intake. This is the case because having a large brain and therefore being able to cognitively buffer seasonality involves the ability to respond flexibly in the face of unpredictable challenges posed by the environment, e.g., flexible switching to alternative food resources. Therefore, relatively large-brained species exhibit less seasonal variation in energy intake than the seasonality of their habitat would suggest. The *Cognitive Buffer hypothesis* (Allman et al., 1993; Deaner et al., 2003; Sol, 2009) predicts that living in more seasonal habitats favours the evolution of relatively larger brains, because enhanced cognitive abilities buffer individuals from environmental perturbations by enhancing behavioural flexibility in the face of environmental changes. Thus, larger brained species are expected to outperform smaller brained species in more seasonal habitats, which are more cognitively demanding because food sources are more difficult to (re)locate in space or time or must be extracted from a matrix. Accordingly, larger brained species are more likely to evolve in more seasonal habitats. Evidence for this hypothesis mainly stems from research in birds.

Cognitive buffering in birds

In a comparative study on 99 Neotropical parrot species, relatively larger brains were found to be associated with higher variability in temperature and precipitation (Schuck-Paim et al., 2008). Another much larger comparative study across 1217 bird species found a similar pattern. Larger brains are more likely to occur in bird species exposed to greater variation in environmental conditions throughout their geographic range (Sayol et al., 2016). Indirect evidence that these findings are due to cognitive buffering

comes from studies comparing migrating and sedentary bird species. One of these studies found that species that reside the entire year in highly seasonal regions have larger brains than those that migrate to benign areas during the seasonally lean periods (Winkler et al., 2004; Sol et al., 2005; Vincze, 2016), reflecting a potential cognitive buffering effect in the resident species. Alternatively, the high-energy requirements for a long distance migratory flight may constrain brain size (Isler and van Schaik, 2006; Vincze, 2016, see also migration and habitat switching section below). To sum up, there are two alternative explanations for the finding that sedentary birds have larger brains than migratory species. From an energy-cost perspective, migrating birds have small brains because they might not be able to provide enough energy for a large brain during the strenuous migratory journey (Isler and van Schaik, 2006; Isler and van Schaik, 2009a). On the other hand, from a benefit perspective of a large brain, migratory species must migrate because their small brain makes them inflexible in their foraging behaviour and therefore unable to buffer seasonal food fluctuations through cognitive buffering. Some classical examples in birds provide direct evidence that species living in harsh environments buffer seasonal food scarcity through cognitive abilities such as innovation and learning. One of the most widely cited examples is the “milk bottle” innovation in blue (*Cyanistes caeruleus*) and great tits (*Parus major*), where birds learnt to peck through the foil caps of milk bottles left on doorsteps in order to drink the cream (Fisher and Hinde, 1949; Hinde and Fisher, 1951; Aplin et al., 2013). Another example is the predation on hibernating bats in great tits (*Parus major*) during periods of food scarcity, where the tits specifically and systematically searched for and killed bats for food but substantially reduced this predation on bats when provisioned (Estók et al., 2009). Furthermore, there is some evidence that birds cope with seasonal harshness using cognitive buffering through food-caching. As food-caching is only beneficial if high rates of recovery of cached food items are achieved, which requires specialized cognitive functions (Jacobs and Liman, 1991), food-caching could also be seen as a cognitive buffering strategy. However, previous studies testing for interspecific relationships between whole brain size or brain regions and food-caching provided conflicting results. Some comparative studies found that food-caching in birds was correlated with an evolutionary increase in whole brain size (Garamszegi and Eens, 2004), or an enlargement of brain regions such as the hippocampus which are responsible for spatial memory (Krebs et al., 1989; Roth and Pravosudov, 2009; Roth et al., 2011). But other studies across different bird species failed to find such a relationship (Volman et al., 1997; Brodin and Lundborg, 2003).

Cognitive buffering in mammals

In mammals, food caching may also help to survive periods of food scarcity as caching allows animals to hold food supply constant (Smith and Reichman, 1984, for a review). However, a study in primates failed to find a link between range size or complexity and hippocampal size (Barton and Purvis, 1994). However, other studies found evidence for another strategy of cognitive buffering, but exclusively in primates so far. One suggested strategy of cognitive buffering deriving from the primate literature is that species with relatively large brains might be buffered against periods of scarcity because of their ability to locate ephemeral food sources (Milton, 1988; Janson, 1998). This idea proposed that tracking the locations and ripeness of fruits that are scattered more widely through the forest than leaves need superior spatial and temporal learning abilities (Milton, 1988). Support for this suggestion was found in primates, where folivorous species had smaller brains compared to frugivorous species (Clutton-Brock and Harvey, 1980). However, alternative explanations were not excluded, so the evidence for the idea that primates buffer seasonality by locating scattered ephemeral resources is equivocal at this time.

Based on a comparative analysis of primate studies, Reader and Laland (2002) found a relationship between ecological challenges, including periods of food shortage, and innovation for approximately half of all instances of innovation. A follow-up study found that the frequency of behavioural innovations and particularly of technical innovations involving novel foraging techniques, such as innovative predatory techniques, commensal foraging, tool use and extractive foraging correlated with absolute and relative brain size (Navarrete et al., 2016). These results suggest that large brains allow animals to buffer seasonally lean periods by innovative ways of acquiring alternative foods. Hemingway and Bynum (2005) analysed qualitative data on primate responses to seasonally lean periods from 234 studies covering 119 species and found that most primates (over 70%) respond to food scarcity by changing their diets. Mostly, they switch to alternative, less preferred resources termed "fallback foods", that are abundant but have low profitability, i.e. lower energy return per unit foraging time (Knott, 1998; Marshall and Wrangham, 2007; Vogel et al., 2009; Lambert and Rothman, 2015). But some relatively large-brained and thus cognitively more flexible primates are (also) able to switch to food items that are highly profitable but difficult to acquire, and thus counterbalance an energetic constraint of experienced seasonality on brain size by cognitive buffering. Alberts et al. (2005) studying baboons found that energy intake remained approximately constant throughout the year in spite of a highly seasonal habitat. Bliege Bird and Bird (2005) summarize similar findings for human foragers living in highly seasonal environments. Further support comes from broad comparative studies across different primate species. Thus, van Woerden and colleagues (2010; 2012; 2014) developed a clever way to define cognitive buffering by the difference

between environmental (and thus potentially experienced) and (actually) experienced seasonality. Using this cognitive buffer definition, they found positive relationships between relative brain size and the amount of cognitive buffering in platyrrhine and catarrhine primates, and to a lesser degree also in lemurs. However, in contrast to the bird studies reviewed earlier, no mammal study has found that species have larger brains in more seasonal habitats. This difference may be linked to the relatively high costs of travel for mammals, especially arboreal ones.

In sum, the most convincing evidence for cognitive buffering comes from primate studies providing correlative support that larger-brained species are superior in balancing food fluctuations compared to smaller-brained species. It is likely, but not yet demonstrated, that such buffering requires improved access to hidden and highly nutritional food items. Retrieving these energy-rich food sources, e.g., through extractive foraging or tool use, often involves multiple processing steps, which have to be executed in the correct order and timing. Obtaining these foods is therefore expected to require complex manipulative skills and enhanced cognitive abilities.

Following this line of argument, we would predict a positive correlation between food manipulation complexity and cognitive buffering and hence brain size or intelligence. We examine this relationship in chapter 2 of this thesis. Another important question that remains unanswered so far is why cognitive buffering is particularly prevalent in the primate lineage compared to any other mammalian order. Throughout this thesis, we offer some potential answers to this open question.

Cognitive buffering comes at a cost

Brain size and enhanced cognitive abilities help to avoid starvation during lean seasons if the above mentioned cognitive buffer effects prevail. But the benefit of enhanced cognitive abilities are counterbalanced by energetic demands of larger and hence metabolically more expensive brains. Brain tissue is among the most metabolically costly tissues in the body to maintain and grow (Mink et al., 1981; Rolfe and Brown, 1997; Niven and Laughlin, 2008; Bauernfeind et al., 2014). For instance, humans shunt about 20-25% of all metabolic energy at resting state to a brain that constitutes only 2% of their body mass (Mink et al., 1981). This energy requirement is even higher for neonates, which devote over 60% of their daily energy to their growing brains (Holliday, 1986). This minimal energetic need cannot be temporarily reduced (except probably in deeply hibernating rodents: Krilowicz et al., 1988) (Mink et al., 1981). Consequently, serious energy deficits, as in the case of starvation, leads to permanent brain

damage (Lukas and Campbell, 2000). Thus, brain size is expected to be constrained if in a seasonal habitat the energy supply is periodically too low, even if physiological buffers allow survival (Isler and van Schaik, 2009a). Indeed, orangutan populations living in areas with more frequent El Niño-induced scarcity had relatively smaller brains compared to populations living in more stable environments (Taylor and van Schaik, 2007). Furthermore, comparative studies across primate species found that seasonality in food (and hence energy) intake is negatively correlated with brain size (van Woerden et al., 2010; 2012; van Woerden et al., 2014). A comparative study across non-meat-eating carnivores and rodents found the same negative relationship between environmental seasonality and brain size (Graber et al., in revision). In conclusion, environmental seasonality is both cognitively challenging and energetically expensive. Whether selection favours large brains therefore depends on whether the fitness benefits of having a large brain (probably especially in terms of survival) exceeds the costs of brain maintenance.

Physiological buffering

Body fat storage

An alternative strategy of dealing with seasonal food scarcity is to engage in a physiological buffering strategy, usually involving storing body fat. Fat is the most efficient form of energy storage because 1 g of fat can yield nine calories, whereas 1 g of protein or carbohydrates yields only four calories. In aquatic mammals such as seals and whales body fat can account for up to 45% of body mass (Omura et al., 1971; Pond and Mattacks, 1985; Ryg et al., 1990; Lockyer, 1991; George et al., 2007). In these species, body fat may not only serve as energy reserve but also as thermal insulation (Marino, 1998; Mclellan et al., 2002; Montie et al., 2008; Zeng et al., 2015). But also land-living mammals can reach high levels of body fat in the wild (up to 40% in polar bears (*Ursus maritimus*) (Atkinson and Ramsay, 1995), up to 35% in brown bears (*Ursus arctos*) (Harlow et al., 2002), up to 24% in woodchucks (*Marmota monax*) (Schoenemann, 2004) and in Eurasian badgers (*Meles meles*) (Pond and Mattacks, 1985), and up to 23% in edible dormice (*Glis glis*) (calculated from Navarrete et al., 2011)). All these land-living mammals occupy highly seasonal habitats with large fluctuations in food availability, suggesting that it is essential for them to store fat during seasons of abundance and catabolize these stores during lean periods. Hence, we would expect to find mammals which rely on body fat to buffer food scarcity mainly in extreme climates facing unavoidable starvation where it does not pay off to have a large brain to find hidden food resources because there is just no food available (Isler and van Schaik, 2009a; van Woerden et al., 2010, see also cognitive buffering above).

Adipose tissue contains three types of fat cells – white, beige and brown body fat (Pfeifer and Hoffmann, 2015). The main function of white adipocytes is to store energy as lipids, and they make up the majority of body fat in mammals. The other two types of body fat dissipate energy in the form of heat via the uncoupling of oxygen consumption from ATP production, which mediates nonshivering thermogenesis (Godfrey et al., 2000; Chechi et al., 2013). Brown and beige body fat play an important role in newborn mammals, who use this tissue to defend themselves against a cold environment (Aherne and Hull, 1966; Hull and Hardman, 1970; Rowlatt et al., 1971), although adults often still also possess some metabolically active brown and beige body fat. In adult humans, for instance, brown body fat comprises only around 0.05% of the adult body mass (Nedergaard et al., 2007; Enerbäck, 2010). In other adult mammals, brown fat comprises 0.9% of body mass in deer mice (*Peromyscus maniculatus*) (Roberts et al., 1966), 3% in North American least shrews (*Cryptotis parva*), 1.9% in house shrews (*Suncus murinus*) and 0.2% in Rhesus monkeys (*Macaca mulatta*) (Chaffee et al., 1970). In mammals that hibernate or fall into torpor, brown body fat plays an essential role for arousal (Godfrey et al., 2000 and references therein). In these species, brown body fat can account for a slightly higher percentage of body mass than in non-hibernating species (e.g., 2% in European hedgehogs (*Erinaceus europaeus*) (Carlier and Evans, 1903), 2% in woodchucks (*Marmota monax*) (Rasmussen, 1923), 4.5% in golden mantled ground squirrels (*Callospermophilus lateralis*) (Horwitz et al., 1968), and 3% in thirteen-lined ground squirrels (*Ictidomys tridecemlineatus*) (Joel, 1965)). Nevertheless, even in hibernators and torpid species the majority of body fat is white.

Besides many benefits of body fat, potential fitness costs of having large adipose depots also play a role in explaining interspecific differences in the percentage of body fat. The costs not only involve increased locomotor costs due to higher total body mass and a less optimal body geometry (Browning et al., 2006; Ghiani et al., 2015), but also increased predation risk (or decreased hunting success) due to reductions in agility and speed (Gosler et al., 1995; Dietz et al., 2007; Zamora-Camacho et al., 2014). Due to these fitness costs of adiposity, we expect fewer arboreal or volant species to rely on fat storage to buffer seasonally lean periods than terrestrial or aquatic ones, because flying and climbing involve higher cost of transporting adipose depots than swimming or moving horizontally (Alexander, 2003; Hanna et al., 2008). In chapter 3 of this dissertation, we test this hypothesis.

Hibernation and torpor

Body fat is especially expected to be beneficial for species which hide motionless and safe from predators in secluded dens, burrows or tree holes during the time of high body fatness. This is exactly what hibernating or torpid species do. Daily torpor is characterized by a dormancy bout duration of less than 24 hours, whereas hibernation is a sequence of prolonged torpor bouts that can last up to nine months (Hudson, 1973; Geiser and Ruf, 1995; Lovegrove et al., 2014). Hibernation or torpor clearly are an energetic necessity for many mammal species that reside year-round at temperate latitudes or that exclusively depend on highly seasonal resources such as insects, flush leaves, or fruits (Boyer and Barnes, 1999; Carey et al., 2003). This is particularly true for small non-volant animals, which consistently need high-quality foods and mostly cannot evade adverse conditions by migration. Small mammals need high-energy density diet because in general, smaller endothermic animals have increased energy requirements per unit of body mass owing to the effects of allometric scaling (Rubner, 1883; Kleiber, 1961; White and Seymour, 2003; Glazier, 2005). This is because smaller animals have a greater surface area for their volume. Because of such scaling, smaller animals lose heat at a faster rate than larger animals and therefore have to consume proportional to their body weight more energy in order to keep themselves warm. Therefore, compared to smaller-bodied species, larger-bodied species can not only thrive on foods of lower energy density (e.g., leaves or grass), but they also tolerate fluctuations of energy input better (Oftedal, 2000; Ellison, 2001).

Before the onset of the inactive phase, animals massively increase their food intake and body mass. For instance, Arctic ground squirrels (*Urocitellus parryii*) and yellow-bellied marmots (*Marmota flaviventris*) nearly double their body weight over the summer and 60-80% of this weight increase can be accounted to white adipose tissue, which triples in mass (Galster and Morrison, 1976; Florant et al., 1990). Alternatively, instead of only fattening, species can also augment body fat with food stores, principally seeds, nuts and bulbs, in their hibernacula (Kenagy and Barnes, 1988; Humphries et al., 2002; Kuhn and Vander Wall, 2008). These animals such as chipmunks (*Tamias* spp.), Golden hamsters (*Mesocricetus auratus*), or hazel dormice (*Muscardinus avellanarius*) periodically arouse, feed from their food hoards, and then become hypothermic again (for a review, see Vander Wall, 1990). However, these energy stores, be it body fat or food caches, can only provide sufficient resources for the inactive season because metabolic rate is reduced to as little as 5% of the normothermic level and low body temperature (for a review, see Lyman, 2013).

Although constituting an effective survival strategy, the extended inactivity of animal cells and tissue during hibernation and torpor is coupled with a cost. Hibernating European ground squirrels (*Spermophilus citellus*) showed a lower memory retention than non-hibernating individuals of the same species, and some behaviours even required relearning in the following spring after hibernation (Millesi et al., 2001). A possible explanation for this memory loss might be a reduction in neuronal connectivity during hibernation, as EEG-measurements of torpid animals have shown that almost no brain activity is present (Walker et al., 1977; Krilowicz et al., 1988; Daan et al., 1991). Studies in hibernating ground squirrels and hamsters in torpor show that these species are able to dramatically reduce brain metabolism, to about 1-2% of the normal active levels, changing metabolic pathways from glucose to fat burning (von der Ohe et al., 2006; Osborne and Hashimoto, 2008). This decrease in brain metabolism may negatively affect the maintenance of neuronal connections. Anatomical evidence for a reduced neuronal connectivity during torpor has been found in certain regions of the hippocampus in Arctic ground squirrels (*Urocitellus parryii*) (Popov and Bocharova, 1992; Popov et al., 1992).

The above-mentioned findings indicate negative effects of hibernation and torpor on cognition, which may pose important constraints on animals. For instance, large-brained species such as anthropoid primates (Isler et al., 2008; Isler and van Schaik, 2012), which rely heavily on learning to solve a wide range of complex problems, would be too much impacted by the memory loss occurring during torpor or hibernation. Although it is unknown how memory and learning are affected by torpor or hibernation in primates, only three primate genera are known to show torpor or hibernation (*Cheirogaleus*, *Microcebus,* and *Nycticebus*) (Schülke and Ostner, 2007; Ruf et al., 2015). Furthermore, these three genera are among the smallest-brained primates (Isler et al., 2008), and a possible negative relationship between brain size and torpor/hibernation can be expected.

An alternative hypothesis for why we would expect relatively small brains in hibernating or torpid species is that brain tissue is energetically among the most expensive tissues to maintain (Rolfe and Brown, 1997, see also cognitive buffering above; Niven and Laughlin, 2008). Selection should favour increased brain size only for species which are active throughout the year and hence benefit from using their larger brains continuously. In addition, large-brained species are expected to be behaviourally more flexible in foraging behaviour and dietary breadth (van Woerden et al., 2012, see also cognitive buffering above; van Woerden et al., 2014; Navarrete et al., 2016), while species with relatively smaller brains are not capable of such flexibility and instead might store fat and hibernate.

Decreasing resting metabolic rate

A decrease in resting metabolic rates (*in extremis* leading to hibernation or torpor, see above) is an effective strategy to buffer food deprivation and other seasonal environmental stresses (for a review Guppy and Withers, 1999). Almost all animal taxa adjust resting metabolic rate during certain seasons to save energy (Goldman et al., 1999). The main suggested causes for the decrease in resting metabolic rate are a decline in body mass including a seasonal shrinkage in the braincase and presumably also brain size, along with a size reduction of other organs (also known as the Dehnel effect; Pucek, 1965; Heldmaier, 1989; Korn, 1989; Lovegrove, 2005; Dechmann et al., 2017; LaPoint et al., 2017), a decrease in basal heat production and hence in body temperature (Fuglesteg et al., 2006), a reduction of activity (Jeanniard Du Dot, 2007), an increased insulation through a winter coat (Sheriff et al., 2009), or a change in corticoadrenal, thyroid, and gonadal functions (Ashwell-Erickson and Elsner, 1981; Perret, 1992) during the season of food scarcity. However, these traits have not been investigated in a sufficient number of species to allow for a broad comparative test.

Migration and habitat switching

Another strategy through which mammals cope with environmental seasonality is by seasonal migration, which involves a move into a different habitat so that net energy intake can be maintained (Alerstam et al., 2003). Seasonal migration or range shifting in times of resource scarcity are expected to be more common in mobile taxa such as aquatic or volant mammals compared to substrate-bound animals such as primates or rodents.

Bats are the only mammals to have evolved true flight and therefore can travel over long distances. As bats can switch area quite easily, several bat species use this strategy to buffer food scarcity (McGuire and Ratcliffe, 2011; McGuire and Boyle, 2013). But to sustain flight, they require large amounts of energy, around 15 times basal metabolic rate (Speakman et al., 2003). Some studies have assumed that fat is the primary fuel for migratory flight in bats (O'Shea, 1976; Fleming et al., 2003; McGuire et al., 2012), but there is limited evidence for this assumption. More recent studies found that most bats do feed nightly and therefore fuel flight with recently ingested nutrients (Welch and Suarez, 2008; Ahlén et al., 2009; Reimer et al., 2010; Voigt et al., 2010b; Šuba et al., 2012; McGuire et al., 2013). Other bat species use a mixed fuel strategy relying on these nutrients and endogenous fat stores (Voigt et al., 2012).

On the other hand, McGuire and colleagues (2013) found a reduction of lean body mass in the form of a reduction of the digestive organs of migrating bats, which reduces wing loading and consequently lowers the energetic cost of flight (Boutin and Larsen, 1993; Voigt et al., 2010a). The same study also found changes in adipose tissue composition (higher proportions of polyunsaturated fatty acids) facilitating mobilization and oxidation and providing more energy per fatty acid chain. They also found that bats can even further reduce the high energy demands for migration by using daily torpor during this time.

Brains are energetically expensive (Rolfe and Brown, 1997; Niven and Laughlin, 2008), and the costs of brain function cannot be reduced temporarily (Lukas and Campbell, 2000; Karasov et al., 2004; Bauchinger et al., 2005). However, high-intensity migratory flight also demands a continuous supply of energy. This is expected to result in a trade-off between locomotor costs and brain size. Not surprisingly, migratory bats were found to have smaller brains than sedentary species (McGuire and Ratcliffe, 2011). An alternative explanation for this finding poses that species with relatively smaller brains are not capable of keeping their energy intake relatively constant when food availability varies, e.g. by finding or accessing hidden or protected food sources, and instead migrate to remain within more favourable habitats (see cognitive buffering above). In birds, both hypotheses were found to explain brain size evolution in the context of migration, but on different ends of the migratory spectrum (Sayol et al., 2016; Vincze, 2016).

The other group of mammals which is highly mobile are aquatic species such as whales, dolphins and seals (Cetacea and Pinnipedia). In a fully aquatic lifestyle, large body size and volume due to large fat stores do not increase costs of transport (Marino, 1998; Pond, 1998; Alexander, 2003). Rather than hampering it, fat stores actually enhance locomotor efficiency in aquatic species, which has been demonstrated in several seal species (Beck et al., 2003; Adachi et al., 2014; Richard et al., 2014). Therefore, body fat might be used as primary fuel for migrations even across considerable distances. For instance, blue whales (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*) are suspected to fast or eat very small amounts of food during 5-7 months (Oftedal, 1997). However, contrary to bats, which migrate to avoid low food availability, in whales the reason for seasonal migrations between productive cold-water feeding grounds and the nutrient-poor warm tropical waters is breeding. Females give birth in warm waters because the young only have a thin layer of blubber to keep them warm, and predation risk has also been suggested to be lower in these regions (Corkeron and Connor, 1999; for a review).

Lastly, even some terrestrial mammals within ungulates (Fryxell et al., 1988; Hebblewhite and Merrill, 2009; Teitelbaum et al., 2015) and carnivores (Loucks et al., 2003) are known to switch habitat over several hundreds of kilometres.

Seasonal breeding

Seasonal breeding is an important fitness component for species living in highly seasonal habitats (Bronson, 1985; van Schaik and van Noordwijk, 1985). The adaptive advantage gained by mammals breeding at the most favourable time of the year are an increased chance of survival of the offspring (Côté and Festa-Bianchet, 2001; Soto et al., 2004) as well as an increased future reproduction of both females and offspring (Lancaster and Lee, 1965; Thomas et al., 2001).

As most mammalian species have a relatively fixed gestation length which scales to body mass (Bronson, 1989; Clauss et al., 2014), timing of mating and parturition is also fixed. Very small species generally have short reproductive cycles and are able to fit mating, birthing and infant dependency into the short time window of optimal environmental conditions (Kiltie, 1988; Zerbe et al., 2012). Large-bodied species are not able to fit the whole reproductive cycle into the one time frame of optimal resource availability. In highly seasonal habitats, they evolved a lengthened gestation period to bridge the lag period between favourable mating conditions and favourable birthing conditions (Jabbour et al., 1997). Some species, particularly of moderate size, even evolved a third strategy to time mating, birth and infant dependency to adequate resource availability in seasonal environments. Clades of six mammalian orders (Artiodactyla, Diprotodontia, Cingulata, Carnivora, Rodentia and Chiroptera) evolved delayed implantation (for a review, see Orr and Zuk, 2014) which allows them to relax the tight correlation between body mass and gestation length and uncouple mating and parturition (Sandell, 1990; Ferguson et al., 1996; Thom et al., 2004; Ferguson et al., 2006).

Care buffering

Reproduction is energetically very expensive for most organisms. This is particularly true for placental mammals, where females bear the metabolic costs of gestation and lactation (McNab, 2006; Speakman, 2008). Therefore, we propose a third buffering strategy besides physiological and cognitive buffering: reproductive females may buffer seasonality through allomaternal care by distributing the costs of reproduction over several individuals (*Care Buffer hypothesis*). In chapter 4 we provide evidence for the existence of this buffering strategy.

Similar to this hypothesis, Clutton-Brock (2016) and Smaldino et al. (2013) suggested that cooperative breeding is found more frequently in mammalian species inhabiting harsh environments with low and unpredictable rainfall and food availability. They argue that in these harsher environments natural selection might have favoured allomaternal care because the effort in the form of care that must be exerted to successfully raise young to adulthood are too high for the parents alone and additional help of other group-members is required. Support for a relationship between habitat seasonality and allomaternal care in mammals has recently been reported in a comparative study which found that cooperative breeding species live more often in arid, unpredictable environments (Lukas and Clutton-Brock, 2017).

Studies in birds also found support for the above-mentioned ideas. Comparing 36 different plover populations (*Charadrius spp.*), researchers found that male care increases with both mean ambient temperature and temperature stochasticity and that local climatic conditions therefore explain within-species population differences in parental cooperation (Vincze et al., 2016). Jetz and Rubenstein (2011) (see also Rubenstein and Lovette 2007) found in comparative studies that cooperative breeding is likely an adaptation to temporally variable, but seasonal, environments (but see Gonzalez et al., 2013, for a counter-example). Another social mode, family living, was also found to have evolved in response to seasonally occurring unfavourable conditions in birds (Drobniak et al., 2015). However, an even larger comparative study across over 4700 bird species found evidence in the opposite direction: Living in harsh environments does not select for cooperative breeding, but rather, cooperative breeding facilitates the colonization of harsh environments (Cornwallis et al., 2017).

Care buffering is expected to be especially beneficial for species with large brains, as a relatively large-brained mother has to both support her own brain and provide energy for the large-brained offspring (Isler and van Schaik, 2009b; Isler, 2011; Isler and van Schaik, 2012). We further expect species to use this Care Buffer strategy if the alternative fuel for reproduction, body fat, entails large fitness costs. Body fat is costly for most non-aquatic mammal as large fat reserves increase the energy costs of locomotion due to higher body weight , and also reduce agility and speed and so may compromise fitness by increasing predation risk or decreasing hunting success (see section body fat storage above). Therefore, we hypothesize that most non-aquatic female mammals should minimize the amount of fat stores if they have an alternative to fuel their reproductive success (for exceptions see general discussion of this thesis). But because flying and climbing involve higher cost of transporting adipose depots than swimming or moving horizontally (Alexander, 2003; Hanna et al., 2008), we would expect even higher amounts of allomaternal care in arboreal and volant species.

Content and aims of this dissertation

The overall aim of this thesis is to broaden the existing knowledge on three different strategies mammalian species use to buffer seasonal food scarcity, in order to draw inferences regarding the role of seasonality in the evolutionary history of our own species.

Environmental changes and its effect on food fluctuations has been argued to be a major selective factor in hominin radiation (Vrba, 1985; Foley, 1993; Rogers et al., 1994; Isbell and Young, 1996; Brockman, 2005; Wrangham, 2009). Environmental fluctuations have already become more extreme since the late Miocene, around six million years ago, as the climate started to become cooler and dryer (DeMenocal, 1995; Potts, 1998). Around 2.5, 1.7 and 1.0 million years ago even more extreme climatic oscillations occurred (DeMenocal, 1995; deMenocal and Bloemendal, 1995). Furthermore, more recently, humans dispersed out of Africa and began to colonise latitudes beyond the subtropics until they occupied the majority of global regions (Malaspinas et al., 2016; Mallick et al., 2016; Pagani et al., 2016), thus exposing them to different climatic stresses and more pronounced levels of seasonality. The implication of all these studies is that very likely the whole hominin evolution including the evolution of our own species, *Homo sapiens*, has occurred entirely within a period of intense fluctuations in environmental seasonality.

Three traits, brain size (cognitive buffering), body fat (physiological buffering) and allomaternal care (care buffering), have consistently been suggested as strategies through which early and modern humans buffer environmental seasonality (Kaplan et al., 2000; Wells and Stock, 2007; Wells, 2010; Smaldino et al., 2013). However, in contrast to living mammalian species, it is difficult to assess whether extinct hominins did indeed buffer seasonality with one or several of these three strategies, because behaviour and soft tissue such as adipose depots are generically absent from the fossil record. Therefore, throughout this thesis we rely on knowledge about how mammals, including our closest relatives, the primates, buffer seasonality in order to shed light on the role seasonality might have played during human evolution.

This dissertation is based upon three main chapters representing original research. Each chapter has been written to stand independently and either has been published or will be submitted to scientific journals. A brief overview of each chapter is given below:

Chapter 2: Manipulation complexity in primates coevolved with brain size and terrestriality

In chapter 2, I empirically examined whether primates with relatively large brains are able to use more complex manipulations to acquire food than smaller-brained species. We found that food manipulation complexity was particularly high in species that use cognitively challenging food acquisition techniques, such as extractive foraging and tool use. Manipulation complexity was also consistently positively correlated with brain size and cognitive test performance. This findings lends support to the idea that large brains enable primates to keep their energy intake constant despite environmental fluctuations in food availability (cognitive buffering), e.g., by finding or accessing hidden or protected food sources that require coordinated and complex processing techniques. Furthermore, we found that terrestriality had a positive effect on the relationship between manipulation complexity and brain size and that humans reached by far the highest manipulation complexity of all primates observed, even higher than predicted for our brain size. Thus, in human evolutionary history, the combination of terrestriality with bipedality may have boosted a positive feedback loop with manipulation complexity, far beyond the range of other primates, combined with an unusually large brain and the corresponding cognitive abilities.

Chapter 3: Being fat and smart: A comparative analysis of the fat-brain trade-off in mammals

In chapter 3, I investigated how physiological and cognitive buffering are linked. Mammalian species that rely on storing fat to survive lean periods are expected to be less active because of increased costs of locomotion and predation. Because this consequence of a fat-storage strategy reduces the net cognitive benefit of a large brain without reducing its cost, such species should be less likely to evolve a larger brain than non-fat-storing species. We therefore predicted that the two strategies to buffer food shortages (storing body fat and cognitive flexibility) are compensatory, and therefore predicted negative co-evolution between relative brain size and seasonal variation in body mass. This trade-off was expected to be stronger in predominantly arboreal clades compared to terrestrial ones, because climbing involves higher costs of transport for additional adipose depots than moving horizontally. Using phylogenetic comparative analyses across of 120 mammalian species, we did indeed find a significant negative correlation between brain size and coefficient of variation (CV) in body mass as a proxy for the tendency to store body fat in the subsample of arboreal species. In predominantly terrestrial species, in contrast, this correlation was not significant.

The results lend support to our prediction that encephalisation (cognitive buffering, active strategy of survival) and fat storage (physiological buffering, passive strategy of survival) are compensatory strategies to buffer against seasonal starvation, unless the reduced cost of transport of additional body fat, as in terrestrial species, alleviates this trade-off and thus allows organisms to combine both strategies. The findings of this chapter help to understand how early humans managed to thrive in increasingly seasonal habitats by combining both strategies: cognitive buffering for example by extractive foraging and tool use and physiological buffering by storing body fat.

Chapter 4: Getting fat or getting help? How female mammals cope with energetic constraints on reproduction

In chapter 4 we propose, besides physiological and cognitive buffering, a third buffering strategy employed by female mammals to buffer seasonally lean periods: Reproductive females may buffer seasonality through receiving allomaternal care, which distributes the costs of reproduction over several individuals (*Care Buffer hypothesis*). If care buffering exist, we would predict that in species where costs of reproduction are distributed over other individuals such as fathers or non-breeding group members, reproductive females might benefit from storing less energy in the form of body fat (for the potential fitness costs of having large adipose depots, see above). Using a comparative approach based on 87 mammalian species, we found that in species with allomaternal care, reproductive females exhibit reduced seasonal variation in body mass, which is a good proxy for the tendency to store body fat. The effect was most pronounced for carrying and provisioning of the young, the presumably energetically most costly allomaternal care behaviours. These results show that both storing fat and allomaternal energy subsidies independently stabilise the energetic costs for female reproduction in seasonal habitats. Humans seem to be an exception to this pattern as we have both a relatively large amount of body fat and intensive allomaternal care. In chapter 5 I will discuss this human peculiarity.

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Chapter 2

Manipulation complexity in primates coevolved with brain size and terrestriality

Sandra A. Heldstab, Zaida K. Kosonen, Sonja E. Koski, Judith M. Burkart, Carel P. van Schaik, Karin Isler

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Abstract

Humans occupy by far the most complex foraging niche of all mammals, built around sophisticated technology, and at the same time exhibit unusually large brains. To examine the evolutionary processes underlying these features, we investigated how manipulation complexity is related to brain size, cognitive test performance, terrestriality, and diet quality in a sample of 36 non-human primate species. We categorized manipulation bouts in food-related contexts into unimanual and bimanual actions, and asynchronous or synchronous hand and finger use, and established levels of manipulative complexity using Guttman scaling. Manipulation categories followed a cumulative ranking. They were particularly high in species that use cognitively challenging food acquisition techniques, such as extractive foraging and tool use. Manipulation complexity was also consistently positively correlated with brain size and cognitive test performance. Terrestriality had a positive effect on this relationship, but diet quality did not affect it. Unlike a previous study on carnivores, we found that, among primates, brain size and complex manipulations to acquire food underwent correlated evolution, which may have been influenced by terrestriality. Accordingly, our results support the idea of an evolutionary feedback loop between manipulation complexity and cognition in the human lineage, which may have been enhanced by increasingly terrestrial habits.

Keywords: manipulation complexity, cognitive abilities, terrestriality, diet quality, brain size, comparative approach

Introduction

Humans stand out among animals in having both a very complex foraging niche, built around sophisticated technology, and an unusually large brain. Is this combination just a coincidence, or instead the product of correlated evolution, as suggested by the relationship between use and manufacture of tools and brain size (Parker and Gibson, 1977; Barton, 2012)? In carnivores, no correlation between brain size and forelimb dexterity during feeding was found (Iwaniuk et al., 1999). Here, using a new method of assessing manipulation complexity in food-related contexts, we examine the relationship between foraging niche complexity and brain size for 36 non-human primate species from various taxonomic groups.

Manipulation complexity was previously defined according to a variety of contrasts: (i) the use of one hand rather than two hands in bimanual coordination; (ii) asymmetrical bimanual manipulation (i.e., both hands simultaneously performing different actions) versus symmetrical bimanual manipulation (i.e., both hands simultaneously performing the same action); (iii) uncoordinated two-handed patterns (i.e. both hands performing actions, independently) versus coordinated two-handed patterns (i.e. both hands performing actions dependent on each other in space and/or time); or (iv) any combination of these criteria (Elliott and Connolly, 1984; Hopkins and de Waal, 1995; van Schaik et al., 1999; Byrne, 2005; Leca et al., 2011). However, in all these reports on how primates use their hands to perform object manipulation, no explicit evaluation of the level of complexity was undertaken. Therefore, our first aim was to test whether distinct food manipulation categories can be ranked cumulatively across species according to their difficulty. We can speak of “manipulation complexity” if there is a clear ranking pattern, that is if species which are able to perform a given type of manipulation are also able to perform all manipulations of a lower rank. Such an empirical evaluation of complexity, without a priori assumptions of which manipulations are more complex than others, has to our knowledge not yet been undertaken.

Second, we tested whether a species’ manipulation complexity is related to cognitively challenging food acquisition techniques, such as, extractive foraging or tool use (Parker and Gibson, 1977; Biro et al., 2003). Effective extractive foraging is likely to require complex manipulative skills, because finely tuned movements are an advantage for removing and holding food or manipulating it with different objects. Tool use, on the other hand, is considered cognitively and manipulatively difficult as it often involves bimanually coordinated actions causally relating two or more external objects (Tomasello and Call, 1997).

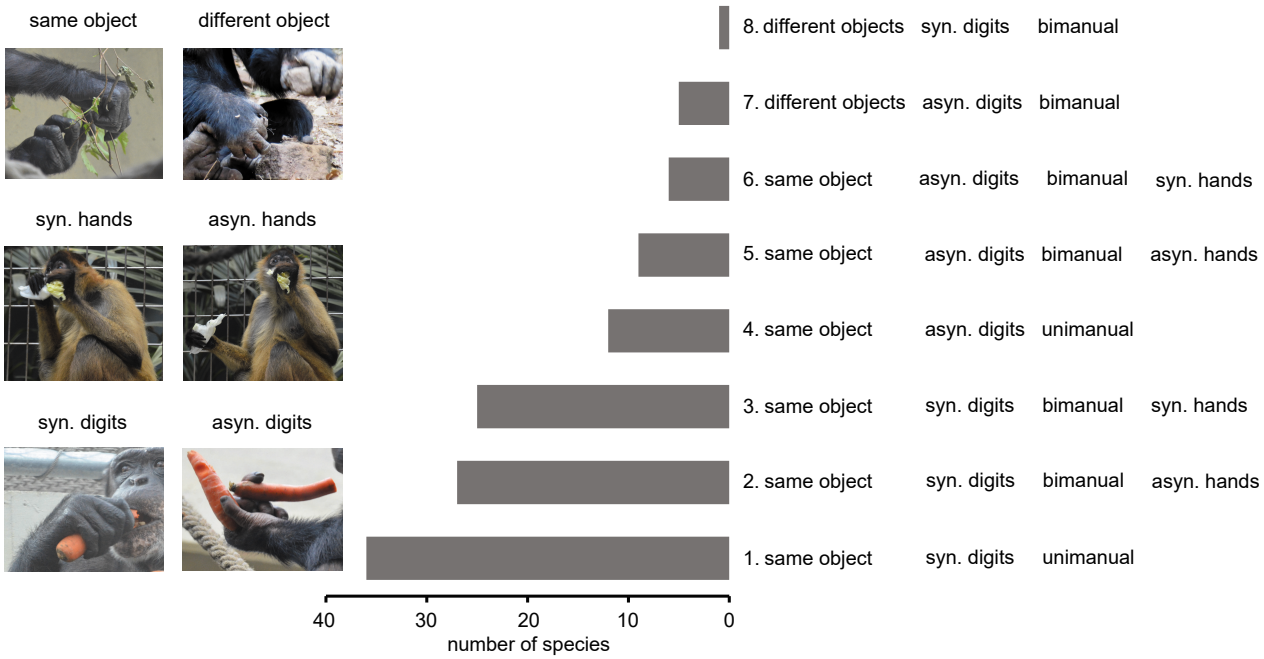

Figure 1. The eight manipulation complexity categories found through the Guttman scaling method (increasing complexity from category 1 to category 8), and the number of species able to perform actions in a particular manipulation complexity category. Copyright S.A. Heldstab, *Pan troglodytes* nut cracking K. Koops.

Third, an emerging consensus is that foraging skills have played an important role in cognitive evolution (Parker and Gibson, 1977; van Schaik et al., 1999; Reader et al., 2011; Barton, 2012; Melin et al., 2014). We therefore also tested whether the degree of food manipulation complexity is related to brain size or cognitive test performance.

We further tested the influence of other factors that may have affected the correlated evolution between brain size and manipulation complexity: diet quality and terrestriality (Byrne, 1997). High-quality diets may require more complex motor and cognitive skills than low-quality diets. For example, insectivorous and frugivorous primates may need to perform more complex manual food processing than folivorous primates, and are more likely to use tools (Melin et al., 2014). Likewise, in a terrestrial habitat, in contrast to arboreal contexts, hands are less commonly needed for positional support, which may allow for the evolution of morphologies capable of more actions on objects and the use of complex actions that require the coordinated involvement of both hands (Fragaszy and Visalberghi, 2004). In addition, discarded tools remain close to where they are used in terrestrial settings, while they tend to disappear from sight after being dropped in arboreal ones (Gunst et al., 2010; Meulman et al., 2012).

If manipulation complexity and brain size coevolved among primates, and thus ecological requirements partly drove brain size evolution in this lineage, it is interesting to ask whether the human manipulation complexity score fits into the pattern based on the relationship between manipulation complexity and brain size in nonhuman primates. If humans fit the primate trend, this suggests that the process of correlated evolution between brain size and foraging ecology may also have played a major role in human brain evolution.

Material and methods

Data collection

We assessed manipulations in food contexts in captive individuals of 36 primate species. All subjects were housed in their home enclosures in single-species groups of 2 to 27 individuals that included at least one adult male and one adult female, except for *Saimiri sciureus* (seven males), *Propithecus verreauxi* (two males, each housed together with a *Eulemur mongoz*) and *Leontopithecus rosalia* (one male). We sampled all available individuals, but immatures were excluded because their manipulation patterns are usually qualitatively different from those of adults (Fragaszy and Visalberghi, 2004; Gunst et al., 2010). Data on human manipulation complexity was collected in a similar way, observing everyday food consumption in a "natural" setting (in the cafeteria of the University of Zurich, Switzerland).

Data were collected by behavioural sampling between October 2011 and February 2014, for a total of 112 hours in various zoos. Manipulation was defined as making physical contact with a food item with the forelimbs, and thus did not include visual exploration or sniffing without contact. Behavioural sampling was conducted in bouts; a bout started as soon as an individual started to manipulate a food item and ended when contact was terminated or after a maximal duration of 5 minutes. After each individual bout, there was an interval of at least 2 minutes without sampling. At least 10 bouts per sex, and thus 20 bouts per species, were collected for most species. In total, 962 bouts were recorded.

Observed manipulation bouts were divided into eight categories. These categories were based on all possible combination of the following: (i) use of the forelimbs, subdivided into unimanual and bimanual actions, (ii) asynchronous and synchronous use of hands, and (iii) asynchronous and synchronous use of digits. Furthermore, in bimanual actions we distinguished between the hands manipulating the same object or different objects, e.g. whether hands were both manipulating a fruit (same object) versus one hand is manipulating with a stick and the other hand is holding the fruit (different object) (Fig. 1).

We only scored the presence of manipulation categories if the observed individuals of a primate species performed a manipulation category at least twice. Frequency or duration of manipulation categories were not assessed.

Agreement between the two observers (inter-observer reliability) was assessed with the kappa statistic (Cohen, 1960), which corrects for agreement due to chance and was applied to the entire coding scheme. The acceptance criterion was set at 0.70, and all kappa statistics were substantially above this basal criterion (manipulation observed: K = 0.85, n = 20; level of manipulation: K = 0.72, n = 18; context of manipulation: K = 0.94, n = 18). Moreover, each species was observed by both observers together for at least 10 minutes to ensure reliability between different species.

Complexity levels

Using the deterministic Guttman scaling method based on the description of Green (1956), we assessed whether the manipulation categories followed a cumulative ranking. Using Guttman's scaling method (Guttman, 1944) we can derive a rank order in a given set of skills, yielding a difficulty scale that is as cumulative as possible. The manipulation skills are ranked such that if an individual is able to perform a particular skill N, then that individual must also be able to perform all or most easier skills < N. Thus, in the ideal case of perfect nesting, if an individual's score is known, this predicts the individual's performances in all skills in the scale. For any empirical set of observed skills, the coefficient of reproducibility (Guttman, 1944) indicates to which extent the skills indeed do fit such a cumulative scale, or, in other words, whether there is a level of difficulty or complexity of the respective skills.

After ranking complexity levels of manipulations using the Guttman scale using all data on all species, mean manipulation complexities were calculated for each species as follows: For each manipulation bout the highest rank reached during the bout was determined. The mean complexity score for each species was then averaged over all observed bouts.

Additionally, we also performed all analyses using the highest manipulation complexity score reached over all observation bouts for each species. The results using this highest manipulation complexity score are largely identical to those obtained with mean complexity scores, but there is a ceiling effect and thus fewer distinctions between species (Supplementary Table S4).

Cognitive test performance and brain size

Two different meta-analyses of cognitive performance of a broad set of primate species provide quantitative estimates of cognitive test performance across primate genera (Deaner et al., 2007; Reader et al., 2011). Using the mean manipulation complexity for each genus (n = 15 genera for Deaner et al. (2007) / n = 19 genera for Reader et al. (2011)), this allows for a direct test of a relationship between manipulation complexity and cognitive test performance on the genus level.

Endocranial volumes of mostly wild-derived female primates (Isler et al., 2008) were used as a proxy of brain size on the species level (n = 36). To remove allometric effects of body size, female body mass was integrated as an independent variable in all multiple regression analyses (Freckleton, 2002). Results showing that brain size is related to cognitive abilities in our primate sample are shown in Supplementary Table S3.

To test whether manipulative skills are particularly high in species known to perform cognitively challenging food acquisition techniques, tool use and extractive foraging were coded as binary variables (present = 1, absent = 0) for each species with data from the literature from wild primates (Gibson, 1986; Myers et al., 2006; Jaeggi and van Schaik, 2011; Rowe and Myers, 2011). In addition, we analysed correlations of manipulation complexity with neocortex and cerebellum size and with foraging group size as a measure of social complexity (results are reported and discussed in detail in the Supplementary material).

To test whether the human manipulation complexity score fits into the pattern between manipulation complexity and brain size in nonhuman primates, we conducted a bootstrapping analysis. The mean and width of the 95% confidence intervals were generated for sample estimates by bootstrapping (1000 iterations) (Efron and Tibshirani, 1993). At each iteration, a bootstrap sample of 25 and 30 nonhuman primate species was constructed by sampling at random without replacement. In a next step we tested whether the estimate of the phylogenetic generalized least-squares regression including the human manipulation complexity score was within the confidence limits calculated on the basis of nonhuman primates. If the data point for humans lies outside the confidence limits, then humans can be considered significantly different from the nonhuman primate trend with $P < 0.05$ (two-tailed). Furthermore, by using the “predict()” function in the “caper” package (Orme et al., 2013) we calculated the human manipulation score which would be predicted for its brain size on the basis of the relationship between manipulation complexity and brain size in nonhuman primates.

Diet quality and terrestriality

To test whether diet quality is related to manipulation complexity, we integrated diet quality data from wild primates (Rowe and Myers, 2011) (and references therein). Diet quality was determined by using temporal variation in the time spent feeding on diet components (and thus their estimated consumption) as in van Woerden et al. (2010): Monthly mean intake of each food category, as estimated by feeding time, was multiplied by its relative energetic quality (8 for insects; 5 for fruits, seeds, and flowers; 3 for gum and young leaves; and 1 for mature leaves, as calculated from g crude fibre/kg dry matter by Langer and Yoder (2003). Fibre content is commonly used as a measure of digestibility and thus energy gained per unit time (McNab, 2002). An alternative, categorical scheme of main diet categories was defined as follows: Insectivorous and frugivorous primates are coded as 1 (diets requiring complex manipulation), and folivorous and gummivorous primates are coded as 0 (diets requiring less complex manipulation). Results using this alternative, categorical scheme of main diet categories are largely identical to those obtained with diet quality, and diet categories are highly correlated because diets related to complex manipulations, such as fruits and insects, also have higher nutritional values (Supplementary Table S7).

As a proxy of terrestriality, primate species were placed in one of three categories based on their main travel habit, as follows: (1) terrestrial (more than 60% terrestrial), (0.5) partly terrestrial (more than 20% terrestrial) and (0) arboreal. Data on terrestriality were taken from the published literature (Myers et al., 2006; Rowe and Myers, 2011).

Statistical analyses

All statistical analyses were performed using JMPTM 10.0 (SAS Institute Inc, 1989-2016) and R2.13.1 (R Core Team, 2015). The method of phylogenetic generalized least-squares regression (PGLS) (Martins and Hansen, 1997) with the “caper” package (Orme et al., 2013) was used to control for phylogenetic non-independence. Phylogeny was based on a composite supertree including branch length estimations (Perelman et al., 2011) (Supplementary Fig. S2). Results using an alternative phylogenetic tree (phylogeny based on version 3 of 10K trees (Arnold et al., 2010)) remained largely similar (Supplementary Table S8). The values of body mass, brain size and diet quality were $\log_e$ transformed in order to reach residuals evenly distributed around zero.

Manipulation complexity of species that use tools or do not use tools as well as of species with or without extractive foraging was compared using PGLS. The correlation of cognitive test performance scores, brain size, diet quality, and terrestriality with manipulation complexity was tested for each variable separately. In a second step, a multiple regression model was run to include manipulation complexity as the response, brain size as effect, and diet quality, terrestriality and body mass as covariates. As diet quality data was not available for *Ateles fusciceps* and *Saguinus imperator*, those two species were excluded from the multiple regression models, yielding a sample size of n = 34 non-human primate species. To choose the best fitting from a set of models, the AIC values (Akaike Information Criterion (Akaike, 1974)) of different models were compared. In these models, we also tested for interaction effects between the predictor variables. Bivariate plots of manipulation complexity against brain size, cognitive test performance, diet quality residuals (corrected for body mass), and terrestriality are shown for illustrative purpose only.

Ethical statement animals

All the observations were carried out in accordance with the Swiss legislation on animal experimentation and formally approved by the Kantonales Veterinäramt of Zurich.

Ethical statement humans

All the observation were carried out in accordance with the Swiss legislation on research involving human subjects. The subjects provided written informed consent, and the observations were approved by the Ethikkommission für psychologische und verwandte Forschung of the Philosophische Fakultät der Universität Zürich (step 1).

Results

We found that manipulation categories follow a cumulative ranking (Fig. 1). In total, 86% of species' performances exactly fitted the resulting Guttman scale, and the coefficient of reproducibility was close to 1 (0.92), indicating that manipulation complexity is indeed cumulative across species. For example, species that are able to perform category 4 mostly also exhibit categories 1, 2, and 3, therefore category 4 can be seen as more complex than the latter.

The scale implies the following scale of manipulative complexity: First, manipulating two objects simultaneously is more complex than manipulating only one object with both hands. Second, the complexity of a manipulation increased with the capability to move digits asynchronously, and when using both hands instead of just one hand for the action. Third, manipulations with synchronous hand use tended to be more complex than manipulations with asynchronous hand use.

Manipulation complexity was significantly higher (P = 0.020) in primate species that regularly use tools and substantially higher (P = 0.056) in species that exhibit extractive foraging (Table 1, Supplementary Fig. S2). Manipulation complexity was also positively correlated with relative brain size (Table 2, Fig. 2) and with performance on cognitive tests (Table 1, Supplementary Fig. S3).

From visual inspection, the relationship between manipulation complexity and brain size appeared to be steeper in terrestrial species, but the effect of the interaction was not statistically significant (Table 2 and Supplementary Table S1, Fig. 2 and Supplementary Fig. S3). Diet quality did not affect the relationship between manipulation complexity and brain size (Table 2 and Supplementary Fig. S3).

Humans reached by far the highest manipulation complexity score of all tested species. Including *Homo sapiens* in the analyses increased the magnitude and significance of the difference in manipulation complexity between species that use tools (P = 0.006) and perform extractive foraging (P = 0.048), compared to species that do not (Table 2 and Supplementary Table S2). Furthermore, the human data point always lies above the upper confidence limit calculated using the relationship between manipulation complexity and brain size of nonhuman primates. This indicates that the human manipulation complexity score and brain size were higher compared to nonhuman primates (Table 3). The human manipulation complexity score calculated using the bootstrapping approach, on the basis of nonhuman primates, was 4.98, which is below the actual measured score of 5.40. Therefore, the human manipulation complexity score was higher than predicted for our brain size, and additional factors (e.g. bipedality, see discussion) may have enhanced human manipulative skills.

Table 1. PGLS models with manipulation complexity as response variable and tool use, extractive foraging or cognitive test performance as explanatory variables. Significant effects are highlighted in bold face.

data set	*n*	λ	adj. r^2	predictor variable	estimate	std. error	*P*-value
excl. *Homo sapiens*	36	0.694	0.125	tool use	0.917	0.374	**0.020**
incl. *Homo sapiens*	37	0.731	0.172	tool use	1.052	0.361	**0.006**
excl. *Homo sapiens*	36	0.760	0.077	extractive foraging	0.520	0.263	0.056
incl. *Homo sapiens*	37	0.808	0.081	extractive foraging	0.554	0.271	**0.048**
Deaner et al. (2007)	15	0	0.552	cog. performance	0.983	0.230	**<0.001**
Reader et al. (2011)	19	0.444	0.396	cog. performance	0.566	0.158	**0.002**

Significant effects are highlighted in bold face.

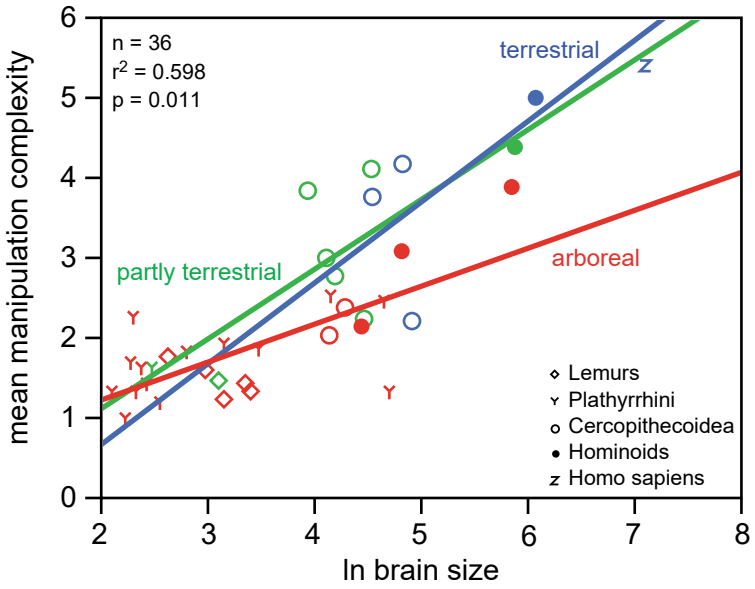

Figure 2. Relationship between manipulation complexity and ln (brain size), for various types of substrate use (raw species values, blue = terrestrial, green = partly terrestrial, red = arboreal) shown for visualization purpose. *Homo sapiens* is not included in the calculation of the correlation and is only shown for illustrative purposes. Statistics see Table 2.

Table 2. PGLS models with manipulation complexity as response variable and brain size as explanatory variables, terrestriality and diet quality as covariates singly and as combined models (*n* = 34, *Homo sapiens* excluded). Body mass is always included as covariate. Significant effects and best-fitting models are highlighted in bold face.

model	*P*-value model	λ	adj. r^2	AIC	ΔAIC	predictor variables	estimate	std. error	*P*-value
model 1	**<0.001**	0	0.728	**60.773**	-	log brain	1.286	0.387	**0.002**
						log body	−0.551	0.312	0.087
						terrestriality	0.948	0.328	**0.007**
model 2	**<0.001**	0	0.721	62.463	1.690	log brain	1.376	0.429	**0.003**
						log body	−0.618	0.346	0.081
						terrestriality	0.927	0.335	**0.010**
						log diet quality	−0.313	0.607	0.610
model 3	**<0.001**	0	0.663	67.105	6.332	log brain	1.274	0.430	**0.006**
						log body	−0.416	0.343	0.234
model 4	**<0.001**	0	0.659	68.438	7.665	log brain	1.422	0.474	**0.005**
						log body	−0.531	0.376	0.165
						log diet quality	−0.513	0.666	0.447
model 5	**<0.001**	0.147	0.567	68.498	7.725	terrestriality	0.863	0.374	**0.028**
						log body	0.439	0.098	**<0.001**
model 6	**<0.001**	0.211	0.461	73.783	13.010	log diet quality	−0.069	0.659	0.918
						log body	0.531	0.101	**<0.001**

Significant effects and best-fitting models are highlighted in bold face.

Table 3. Mean and width of the 95% confidence intervals obtained through bootstrapping.

data set		95 % CI mean	95% CI width
25 species	nonhuman primates	1.205	1.186 - 1.225
	Homo sapiens included	1.294	above the upper CI
30 species	nonhuman primates	1.236	1.224 – 1.249
	Homo sapiens included	1.294	above the upper CI

Discussion

If we aim to understand the evolutionary link between primate manipulative skills and the flourishing of complex technology among humans, we need explicit and consistent operational definitions of manipulative skills as well as a thorough evaluation of the levels of difficulty of the various manipulative actions across a broad variety of primate species (McGrew and Marchant, 1997). Here, we provide manipulation categories that can be easily distinguished, and show that they can be ranked cumulatively according to their complexity across a broad range of primate species, and that this complexity measure is correlated with brain size and relevant ecological aspects (extractive foraging and tool use).

Consistent with previous studies, non-human primate taxa considered to be the most dexterous– specifically chimpanzees (Torigoe, 1985; Hayashi, 2007; Meulman et al., 2012), gorillas (van Schaik et al., 1999; Byrne and Byrne, 2001), orangutans (van Schaik et al., 1999; Byrne, 2005; Meulman et al., 2013), geladas (van Schaik et al., 1999) and macaques (van Schaik et al., 1999; Leca et al., 2011) – also showed high manipulative complexity in our study. These findings support the accuracy of our rankings of the manipulation categories according to difficulty.

Furthermore, the different manipulation categories found in this study correspond quite well to the food processing behaviours observed in wild living primates. For instance, the 72 functionally distinct manipulative actions in wild living mountain gorillas recorded by Byrne and Byrne (2001) would be classified as levels 1 to 6 in our manipulation complexity scheme. But we also observed tool use of level 7 in the captive Western lowland gorillas. Chimpanzees of the Taï National Park (Côte d'Ivoire) (Boesch and Boesch, 1993) and of the Mahale Mountains National Park (Tanzania) (Corp and Byrne, 2002) are able to perform all manipulation categories 1 to 7 found in our study.

Free ranging Japanese macaques (Leca et al., 2011) exhibit asynchronous and synchronous hand and digit use according to complexity levels 1–6 in our scheme, matching our findings for Tonkean macaque and Barbary macaque. The long-tailed macaques, on the other hand, for which we also found level 7 manipulations, are renowned for high manipulation complexity, tool use and extractive foraging in the wild (van Schaik et al., 1999).

Complexity of manipulations

Most previous studies on object manipulation and tool-use in primates were either experimentally induced or directed towards experimentally provided standardized objects (e.g., Torigoe, 1985; Hopkins and de Waal, 1995; Hayashi, 2007). In contrast, in our study, manipulations were unconstrained and undertaken in a non-experimental setting, without introducing new objects or changes to the daily routine of the animals. Animals were free to select food items and any additional objects available within the enclosure. Our data demonstrate that the types of food (sometimes, including chopped fruits or pellets) available to the primates under study did not limit their capacity for manipulations. First, several species exhibited manipulations of high complexity classified in category 7. Second, even species with generally low manipulation complexity showed a few manipulations of higher complexity. Third, species differed in manipulation complexity even when the food items were identical. For example, all primates in the Parc Zoologique et Botanique de Mulhouse (France) were fed with similar-sized chopped fruits. Yet the highest manipulation complexity category ever reached, by different species held in this specific zoo, varied between 1 and 6. In summary, manipulations were not constrained by the availability of a particular food item or object, and all species had the opportunity to show the full range of manipulations.

In our study, the complexity of a manipulation increased when using both hands instead of just one hand for the action. Other studies have indeed found that patterns performed unimanually are more straightforward for the brain to program than patterns performed bimanually (Elliott and Connolly, 1984; Hopkins and de Waal, 1995; Byrne, 2005). For instance, reaching, grasping or holding a food item arise very early in infancy, suggesting a low level of manipulative complexity (Gordon, 2001).

Second, we found that manipulating two objects is more complex than manipulating the same object with both forelimbs. This corresponds to earlier studies on ontogeny of nut cracking in wild chimpanzees. Biro and colleagues (2006) found that in infants in early stages of development interactions with nuts or stones were restricted to the manipulation of single objects on their own, such as holding a stone or rolling a nut. This stage was then followed at later ages by performing actions on multiple objects, indicating that manipulating one object is less complex than manipulating two objects.

Third, the complexity of a manipulation increased with the capability to move digits asynchronously. Again, this pattern also occurs during ontogeny. During human development, individuated movements of the fingers become superimposed on more fundamental grasping movements involving synchronous digits. Reflexive closure of the entire hand, which is present at birth, is followed by voluntary grasping at 2–3 months of age. Thumb opposition and finger individuation start to appear at 10–12 months indicating

that manipulations with asynchronous digits are more complex than with synchronous digits (Gordon, 2001). Furthermore, a study in capuchins showed that they performed manipulation involving synchronous digits much quicker than manipulations involving asynchronous digit use suggesting that using the digits asynchronously seems to be more complex than synchronous digit use (Christel and Fragaszy, 2000).

Fourth, manipulations with synchronous hand use tended to be more complex than manipulations with asynchronous hand use. This finding is surprising as previous studies suggested that patterns of asynchronous hand use are more complex than those of synchronous hand use within species (Elliott and Connolly, 1984; Hopkins and de Waal, 1995; Byrne, 2005). In future studies we will revisit this unexpected result by assessing whether the order of emergence of these manipulation categories during ontogeny matches the order of the complexity scale found in this study.

Ecology

Primate species engaging in extractive foraging and tool use tended to have higher manipulation complexity than those that do not. Previous studies have shown that exactly these two food acquisition modes are mastered relatively late in development, and attributed their late appearance to them being cognitively demanding and involving complex manipulative patterns (Gunst et al., 2010; Meulman et al., 2013). Both suggestions are supported by our results.

Cognitive abilities

Contrary to a study on forelimb dexterity in carnivores (Iwaniuk et al., 1999), we found that in primates brain size and cognitive test performance exhibit correlated evolution with manipulation complexity. This relationship between brain size and manipulation complexity persists even after controlling for foraging group size (Supplementary Table S7). The difference between primates and carnivores may be due to the underlying adaptation for grasping in the primate forelimb. Correlated evolution of brain size and manipulation complexity may be hindered by a phylogenetic constraint of paw morphology in carnivores, a group in which arboreality is only a secondary adaptation. To explain patterns of correlated evolution that shaped brain size variation across mammals, such discrepancies between orders should be studied in more detail.

Additional results on the relationship between the size of specific brain regions (neocortex or cerebellum size) and manipulation complexity showed that relative cerebellum size was not correlated with manipulation complexity (Supplementary Table S5). Relative neocortex size on the other hand was positively correlated with manipulation complexity (Supplementary Table S5). This may indicate a closer link between manipulation complexity and cognitive rather than motor skills. However, the cerebellum is involved not only in sensory-motor control and automatized learning of motor skills, but may also play a role in understanding and producing complex behavioural sequences including tool use (Barton, 2012; Barton and Venditti, 2014). Because our results on brain parts depend on a relatively small sample, they must be regarded with caution.

Terrestriality

The primate pattern suggests that not only full terrestriality, but already a partly terrestrial habit may have positively affected the correlated evolution between manipulation complexity and brain size. The secondary adoption of a partly terrestrial habit may therefore have facilitated innovation by allowing more frequent and repeated actions on objects, as well as the use of complex actions requiring the coordinated involvement of both hands (Fragaszy and Visalberghi, 2004; Meulman et al., 2012). Furthermore, food manipulation complexity in mainly terrestrial species might also be higher as terrestriality affects the availability of food and raw materials to be used as tools (McGrew, 2004; Visalberghi et al., 2005). Terrestrial habitats present a wider range of possible substrates and materials, such as stones and grass stems, in addition to twigs and leaves that can be used as tools (McGrew, 2004; Visalberghi et al., 2005). Similarly, in birds, complex manipulations and tool-use behaviour have been observed in free-ranging species foraging a high proportion of time on the ground, such as ravens and several crow species including New Caledonian crows (Rutz et al., 2007; Emery and Clayton, 2009).

That terrestrial species showed higher manipulation complexity compared to arboreal ones might also be due to the fact that manipulation and locomotion pose different and frequently opposed selection pressures on primate hand morphology. The forelimb-dominated climbing and suspensory behaviours of arboreal species such as e.g. in gibbons favours a long hand functioning as a grasping hook during suspension and/or climbing that is thus less well suited for manipulative functions (Susman, 1979; Inouye, 1992). In contrast, terrestrial quadrupedalism favours a short hand, which is far more compatible with an enhanced thumb/hand relationship, which in turn enables more complex manipulations as in geladas and baboons (Maier, 1993). However, hand morphology alone does not explain manipulation complexity.

The aye-aye (*Daubentonia madagascariensis*), an arboreal species with long digits, especially the thin middle one (D3), would be presumed to have a rather limited capacity for complex manipulations based on its hand morphology. Conversely, in a comparative study, aye-ayes were able to perform more complex manipulations than other lemurs by using the thumbs to secure the food in a sophisticated way (Pellis and Pellis, 2012). This finding demonstrates that fine motor control in the brain can sometimes override motor limitations imposed by body morphology. It is also consistent with our finding that brain size is related to manipulation complexity, since aye-ayes are very large-brained lemurs.

The human case

We also found that humans reach by far the highest manipulation complexity, even higher than predicted for our brain size. Human foragers occupy the most complex foraging niche of all mammals (Schuppli et al., 2012), and forager diet requires intensive processing and relies heavily on enhanced manipulative skills (Kaplan et al., 2000). There is ample fossil evidence that, over the course of human evolution, increasingly bipedal habits freed the hand from the constraints of locomotion and hands could evolve primarily for manipulation, including tool use and eventually tool production (Marzke, 1997; Skinner et al., 2015). The occurrence of human-like hand proportions and features linked to precision grip in very early hominins even hint at the possibility that manipulative skills were an early autapomorphy of the human lineage that co-evolved with habitual bipedalism and was not necessarily related to stone tool production (Panger et al., 2002; Almécija et al., 2010; Almécija et al., 2015). Admittedly, primate species engaging in tool use also showed higher manipulation complexity than those that do not, suggesting that tool use is also involved in enhancing manipulation complexity. However, as the amount of variation in manipulation complexity explained by tool use or extractive foraging is rather small, brain size and terrestriality may be more important factors.

Our comparative evidence also suggests that terrestriality alone already improves manipulative skills. Thus, in human evolutionary history, the combination of terrestriality with bipedality may have boosted a positive feedback loop with manipulation complexity, far beyond the range of other primates, combined with an unusually large brain and the corresponding cognitive abilities. Together with previous findings that terrestriality is crucial for acquiring and maintaining complex tool variants in primates (Meulman et al., 2012), our study lends support to the notion that the combination of intelligence and terrestriality may have been a major pacemaker of hominin technological evolution (Schick and Toth, 1994).

That this simple categorization of manipulation complexity yields a consistent pattern of correlation between processing food and brain size obviously does not rule out that finding food may also play an important role in the evolution of cognitive abilities. Although our results add manipulation complexity to a suite of emerging evidence linking cognition with ecological rather than with social factors (Parker and Gibson, 1977; Byrne, 1997; Barton, 2012; Melin et al., 2014), the outcomes of the present study are also consistent with a role for social factors, as among primates, the developmental acquisition of all complex manipulative skills has a major social-learning component (van Schaik and Pradhan, 2003). However, if social challenges alone (independent of social learning of skills) were responsible for the evolution of the unusually large human brain (e.g., Dunbar and Shultz, 2007), we would expect human manipulation complexity to be lower than expected for our brain size. The fact that the opposite was actually found, is not favourable to the idea that only purely social challenges were involved.

Acknowledgements

We sincerely thank Janneke van Woerden, Erik Willems and Kathelijne Koops for contributing data to our compilation. We are grateful to Rob Barton and Ellen Meulman for their constructive comments. We thank the following zoos for allowing us to collect behavioural data: Bioparco di Roma (Italy), Parc Zoologique & Botanique de Mulhouse (France), and Toni's Zoo, Zoo Basel and Zoo Zurich (Switzerland). Financial support was provided through Swiss National Science Foundation (31003A-144210) and the University of Zurich.

Supplementary material

Supplementary material and methods

Specific brain regions (neocortex and cerebellum)

To test whether manipulation complexity is related to the size of specific brain regions, we examined their correlation with relative neocortex and cerebellum size across primate genera. Some authors argue that relative neocortex size is a better proxy of cognitive ability than whole brain size (Byrne and Corp, 2004). Furthermore, relative cerebellum size may be a better proxy for fine motor skills than whole brain size (Day et al., 2005), but see (Barton, 2012; Barton and Venditti, 2014).

Relative neocortex and cerebellum sizes were available for n = 19 non-human primate genera. The values of neocortex and cerebellum size were $\log_e$ transformed in order to reach residuals evenly distributed around zero.

Social complexity

In this study we do not seek to explain the variation in brain size, but rather variation in manipulation complexity. Nevertheless, the question arises whether sociality may confound the relationship between manipulation complexity and brain size, as suggested by the social complexity hypothesis (Byrne and Whiten, 1988). Therefore, we additionally tested an alternative model with brain size as response and manipulation complexity as effect and the covariates body mass and foraging group size as proxy for social complexity (data from Myers et al., 2006; Rowe and Myers, 2011; Willems et al., 2013; Willems and van Schaik, 2015). The values of foraging group size were $\log_e$ transformed in order to reach residuals evenly distributed around zero.

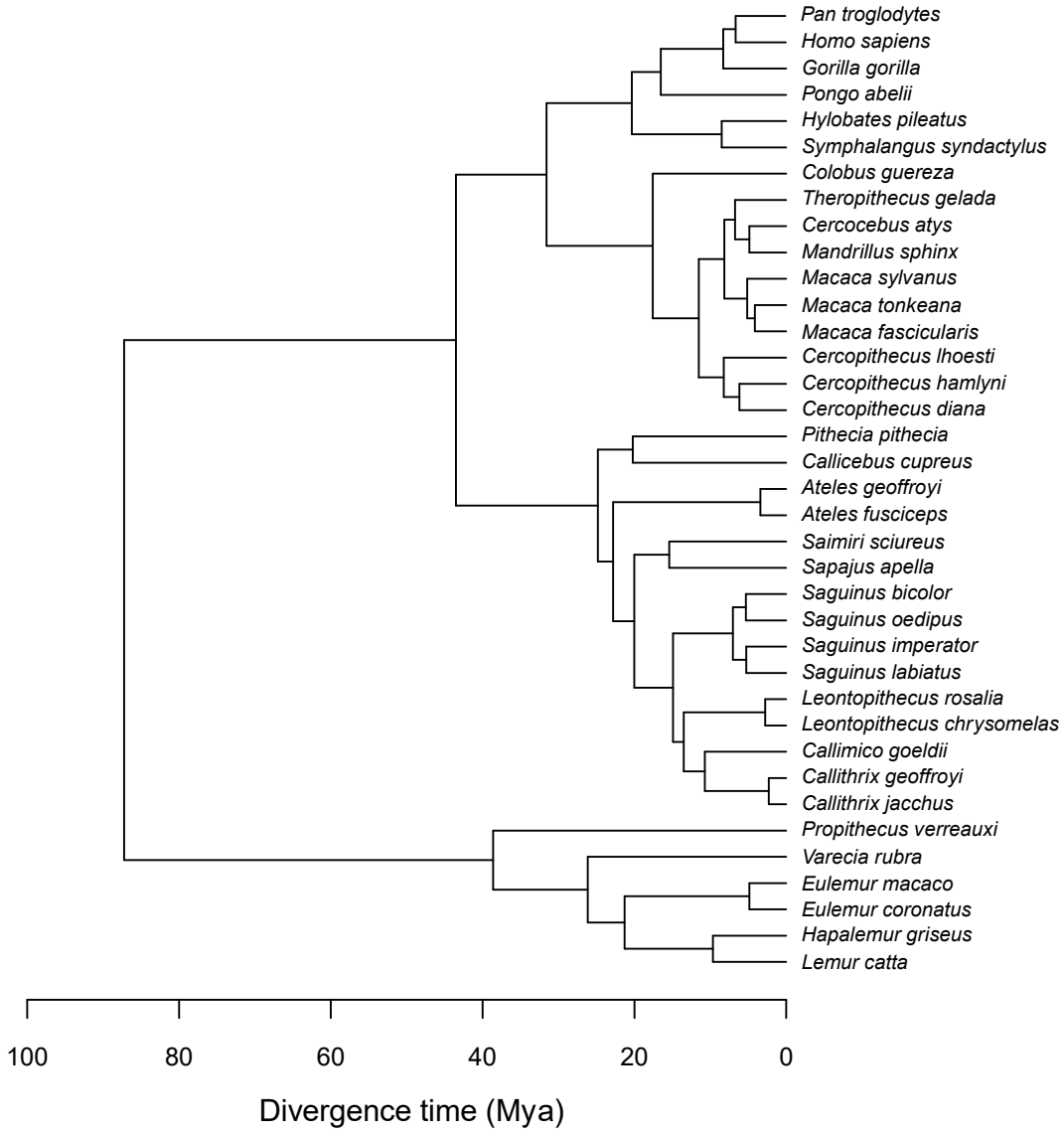

Figure S1. Phylogenetic tree used for the analyses reported in the main text, based on Perelman et al. (2011).

Tree in Nexus format

```
#NEXUS

BEGIN TREES;

        TRANSLATE

                1 Ateles_geoffroyi,                 20 Mandrillus_sphinx,

                2 Callicebus_cupreus,               21 Pan_troglodytes,

                3 Callimico_goeldii,                22 Pithecia_pithecia,

                4 Callithrix_geoffroyi,             23 Pongo_abelii,

                5 Callithrix_jacchus,               24 Propithecus_verreauxi,

                6 Sapajus_apella,                   25 Saguinus_bicolor,

                7 Cercocebus_atys,                  26 Saguinus_labiatus,

                8 Cercopithecus_diana,              27 Saguinus_oedipus,

                9 Cercopithecus_lhoesti,            28 Saimiri_sciureus,

                10 Colobus_guereza,                 29 Symphalangus_syndactylus,

                11 Eulemur_coronatus,               30 Theropithecus_gelada,

                12 Eulemur_macaco,                  31 Varecia_rubra,

                13 Gorilla_gorilla,                 32 Ateles_fusciceps,

                14 Hapalemur_griseus,               33 Cercopithecus_hamlyni,

                15 Hylobates_pileatus,              34 Macaca_tonkeana,

                16 Lemur_catta,                     35 Homo_sapiens,

                17 Leontopithecus_rosalia,          36 Leontopithecus_chrysomelas,

                18 Macaca_fascicularis,             37 Saguinus_imperator;

                19 Macaca_sylvanus,
```

TREE = (((((16:9.66,14:9.66):11.64,(11:4.86,12:4.86):16.44):4.85,31:26.15):12.45,24:38.6):48.62,(((((((5:2.29,4:2.29):8.41,3:10.7):2.80,(36:2.76,17:2.76):10.74):1.40,((26:5.25,37:5.25):1.75,(27:5.3,25:5.3):1.70):7.9):5.1,(6:15.4,28:15.4):4.6):2.80,(32:3.4,1:3.4):19.40):2.00,(2:20.2,22:20.21):4.60):18.72,(((((8:6.16,33:6.16):2.07,9:8.22):3.29,(((18:4.13,34:4.13):0.99,19:5.12):3.02,((20:4.85,7:4.85):1.88,30:6.73):1.41):3.37):6.07,10:17.58):13.99,((29:8.5,15:8.5):11.82,(23:16.5,(13:8.3,(35:6.6,21:6.55):1.65):8.2):3.82):11.25):11.95):43.7):5.0;

END;

Supplementary results

Supplementary results for the correlates of manipulation complexity

Manipulation complexity is significantly higher in primate species that regularly use tools and nearly significantly higher in species that exhibit extractive foraging (Supplementary Fig. S2).

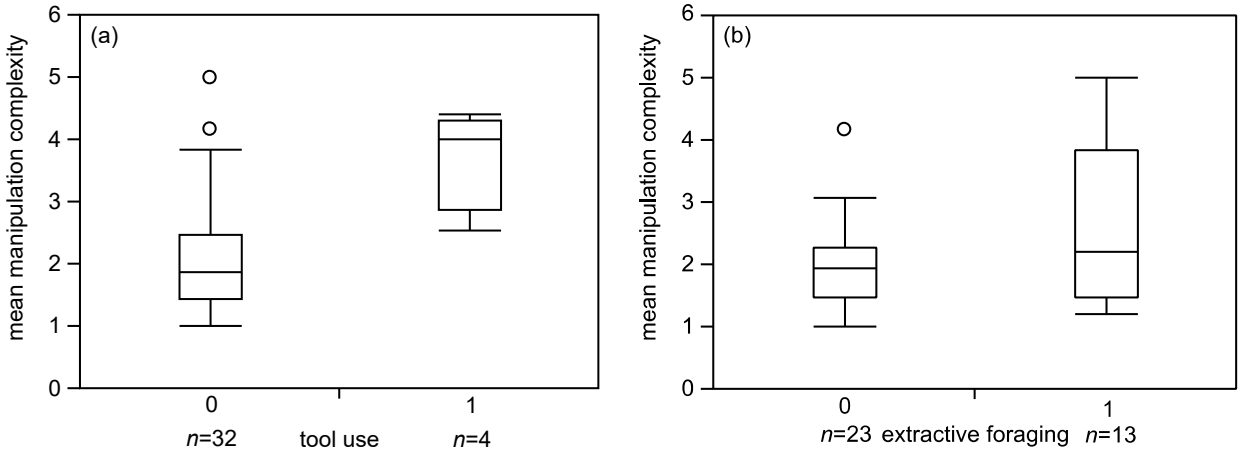

Figure S2. Manipulation complexity (**a**) in primate species that regularly use tools (P = 0.020) and (**b**) in species that exhibit extractive foraging (P = 0.056) (n = 36 primate species, *Homo sapiens* excluded). Statistical details see main text.

Manipulation complexity is correlated not only with relative brain size, but also with cognitive test performance across primate genera (Supplementary Fig. S3). There is no correlation with diet quality (Supplementary Fig. S3).

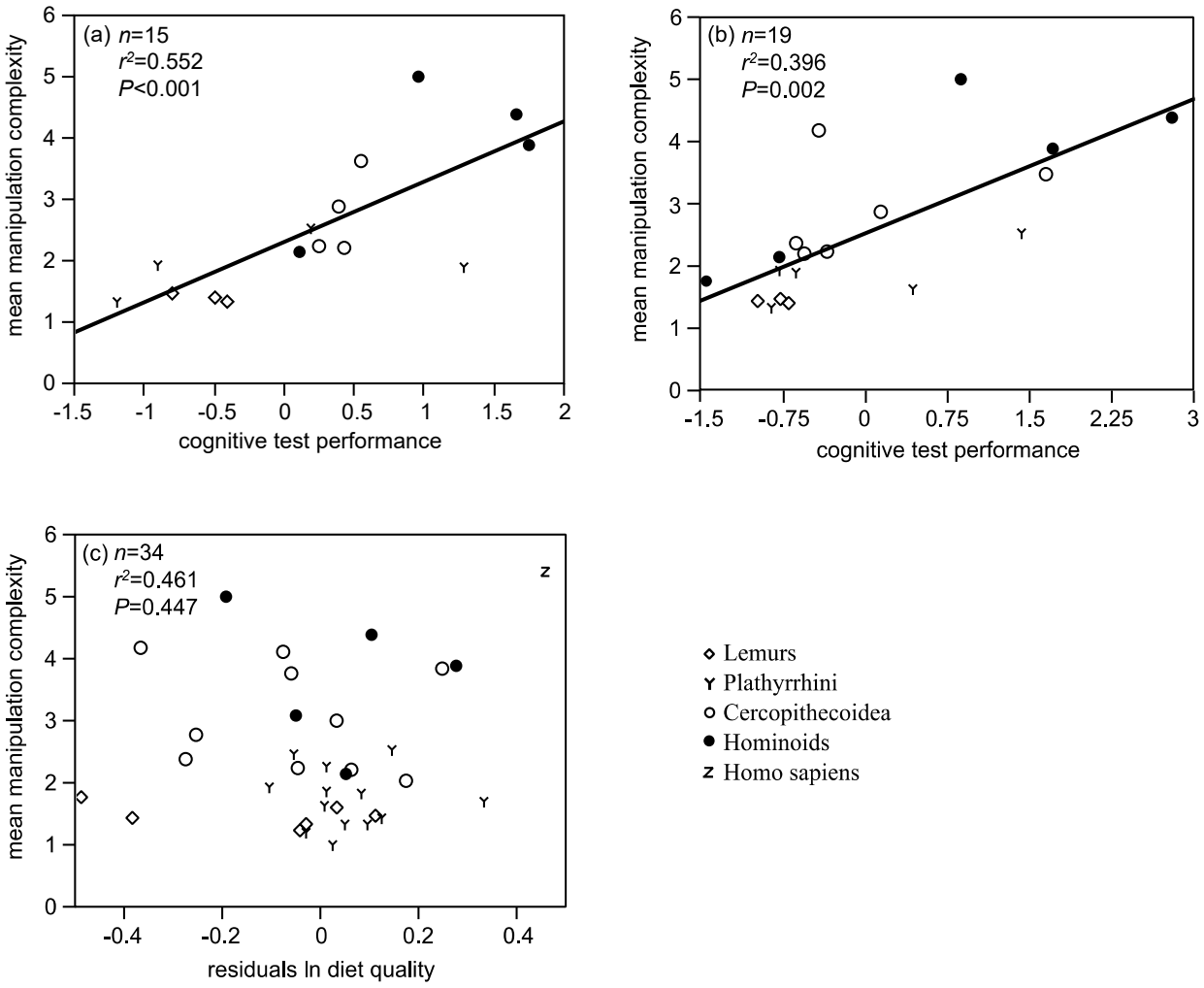

Figure S3. (**a**) Relationship between manipulation complexity and cognitive test performance (raw genus values measured by (Deaner et al., 2007)). Statistical details of the PGLS regression models see Table 1 in the main text. (**b**) Relationship between manipulation complexity and cognitive test performance (raw genus values measured by Reader et al. (2011)). Statistical details of the PGLS regression models see Table 1 in the main text. (**c**) Diet quality (controlled for body mass) and manipulation complexity are not correlated (raw species values). Statistical details of the PGLS regression models see Table 2 in the main text. The symbols denote different primate taxa.

Alternative models, including the interaction terms between brain size and terrestriality and brain size and diet quality, show that the effect of neither interaction is statistically significant (Supplementary Table S1).

Table S1. PGLS models with manipulation complexity as response variable and brain size as explanatory variables, terrestriality and diet quality as covariates singly and as interaction effects with brain size (*n* = 34, excluding *Homo* sapiens). Including body mass as covariate.

***P*-value model**	**λ**	**adj. r^2**	**AIC**	**ΔAIC**	**predictor variables**	**estimate**	**std. error**	***P*-value**
<0.001	0	0.726	61.860	-	log brain	1.175	0.319	**0.003**
					log body	−0.580	0.315	0.076
					terrestriality	0.261	1.400	0.853
					log brain * terrestriality	-0.267	0.301	0.382
<0.001	0	0.683	66.841	4.981	log brain	6.855	3.054	**0.033**
					log body	−0.582	0.375	0.132
					log diet quality	2.691	1.894	0.166
					log brain * log diet quality	−0.877	0.487	0.082

Significant effects and best-fitting models are highlighted in bold face.

The results of PGLS models that include *Homo sapiens* (Supplementary Table S2) are largely similar to those that exclude *Homo sapiens* (Table 2, main text).

Table S2. PGLS models with manipulation complexity as response variable and brain size as explanatory variables, terrestriality and diet quality as covariates singly and as combined models (*n* = 35, including *Homo sapiens*). Including body mass as covariate.

model	*P*-value model	λ	adj. r^2	AIC	ΔAIC	predictor variables	estimate	std. error	*P*-value
model 1	**<0.001**	0	0.778	**61.623**	-	log brain	1.175	0.319	**<0.001**
						log body	−0.471	0.268	0.089
						terrestriality	0.919	0.320	**0.007**
model 2	**<0.001**	0	0.774	63.181	1.558	log brain	1.306	0.386	**0.002**
						log body	−0.584	0.326	0.084
						terrestriality	0.902	0.324	**0.009**
						log diet quality	−0.362	0.586	0.542
model 3	**<0.001**	0	0.728	67.888	6.265	log brain	1.267	0.352	**0.001**
						log body	−0.411	0.296	0.175
model 4	**<0.001**	0	0.725	69.215	7.592	log brain	1.445	0.422	**0.002**
						log body	−0.568	0.360	0.125
						log diet quality	−0.500	0.644	0.444
model 5	**<0.001**	0.157	0.621	71.351	9.728	terrestriality	0.976	0.370	**0.013**
						log body mass	0.460	0.098	**<0.001**
model 6	**<0.001**	0.148	0.551	77.681	16.058	log diet quality	0.455	0.615	0.465
						log body	0.607	0.092	**<0.001**

Significant effects and best-fitting models are highlighted in bold face.

Results showing that brain size is related to cognitive abilities in our primate sample

Deaner et al. (2007) and Reader et al. (2011) showed with large data sets that cognitive abilities are related to brain size in primates. Consistent with these findings also in our study cognitive abilities and brain size are positively linked (Supplementary Table S3).

Table S3. PGLS models with cognitive abilities measured either by Deaner et al. (2007) (*n* = 15) or Reader et al. (2011) (*n* = 19) as response variable and brain size and body mass as explanatory variables.

data set	*P*-value model	λ	adj. r^2	predictor variables	estimate	std. error	*P*-value
Deaner et al. (2007)	**<0.001**	0	0.840	log brain	0.837	0.341	**0.030**
				log body	-0.089	0.270	0.747
Reader et al. (2011)	**0.010**	0	0.371	log brain	1.681	0.786	**0.048**
				log body	-0.889	0.622	0.172

Significant effects are highlighted in bold face.

Results of the highest manipulation complexity score ever reached over all bouts

We conducted additional tests with the highest manipulation complexity score ever reached by a species over all bouts and its relationship to brain size, terrestriality and diet quality. The results of PGLS regression models using this manipulation complexity scoring are reported in Supplementary Table S4. Although P-values vary slightly in comparison with Table 2, on the whole the results are very similar (Supplementary Table S4).

Table S4. PGLS models with the highest manipulation complexity score reached over all bouts as response variable and brain size as explanatory variables, terrestriality and diet category as covariates singly and as combined models (*n* = 34, *Homo sapiens* excluded). Including body mass as covariate.

model	*P*-value model	*λ*	adj. r^2	AIC	ΔAIC	predictor variables	estimate	std. error	*P*-value
model 1	**<0.001**	0	0.611	**104.737**	-	log brain	1.870	0.738	**0.017**
						log body	−0.952	0.595	0.120
						terrestriality	2.132	0.627	**0.002**
model 2	**<0.001**	0	0.598	106.686	1.949	log brain	1.800	0.822	**0.037**
						log body	−0.889	0.675	0.198
						terrestriality	2.148	0.642	**0.002**
						diet category	0.242	1.163	0.836
model 3	**<0.001**	0.113	0.467	108.907	4.170	terrestriality	1.933	0.677	**0.008**
						log body	0.488	0.174	**0.009**
model 4	**<0.001**	0	0.478	113.824	9.087	log brain	1.845	0.855	**0.039**
						log body	−0.648	0.681	0.349
model 5	**<0.001**	0	0.461	115.792	11.055	log brain	1.909	0.950	**0.054**
						log body	−0.708	0.779	0.371
						diet category	−0.223	1.336	0.869
model 6	**<0.001**	0.305	0.234	115.981	11.244	diet category	0.374	1.214	0.760
						log body	0.677	0.198	**0.002**

Significant effects, trends and best-fitting models are highlighted in bold face.

Results and discussion for the relationship between manipulation complexity and relative neocortex and cerebellum size

This section reports additional results on the relationship between the size of specific brain regions (neocortex or cerebellum size) and manipulation complexity (Supplementary Table S5). A positive correlation between manipulation complexity and relative cerebellum size was not found in any model. Relative neocortex size on the other hand was always positively correlated with manipulation complexity. This may indicate a closer link between manipulation complexity and cognitive rather than motor skills. However, the cerebellum is involved not only in sensory-motor control and automatized learning of motor skills, but may also play a role in understanding and producing complex behavioural sequences including tool use (Barton, 2012; Barton and Venditti, 2014). Our results on brain parts, depending on a relatively small sample, must therefore be regarded with caution.

Table S5. PGLS models with manipulation complexity as response variable and neocortex / cerebellum size and body mass as explanatory variables.

data set	*n*	*P*-value model	*λ*	adj. r^2	AIC	ΔAIC	predictor variables	estimate	std. error	*P*-value
excl. *H. sapiens*	19	**<0.001**	0	0.786	**30.132**	-	log neocortex	0.730	0.327	**0.040**
							log body	0.016	0.249	0.950
excl. *H. sapiens*	19	**<0.001**	0	0.791	30.440	0.308	log neocortex	0.960	0.377	**0.023**
							log cerebellum	-0.660	0.559	0.256
							log body	0.366	0.385	0.357
excl. *H. sapiens*	19	**<0.001**	0.468	0.669	33.322	3.190	log cerebellum	-0.323	0.512	0.537
							log body	0.796	0.416	0.073
incl. *H. sapiens*	20	**<0.001**	0	0.845	**30.857**	-	log neocortex	0.857	0.252	**0.003**
							log body	-0.065	0.209	0.761
incl. *H. sapiens*	20	**<0.001**	0	0.844	31.769	0.912	log neocortex	1.088	0.351	**0.007**
							log cerebellum	-0.504	0.532	0.358
							log body	0.167	0.323	0.612
incl. *H. sapiens*	20	**<0.001**	0.230	0.722	38.859	8.002	log cerebellum	0.498	0.453	0.287
							log body	0.192	0.384	0.624

Significant effects are highlighted in bold face.

Results and discussion for a potential confounding effect of social complexity

This section reports additional results of an alternative model testing whether sociality confounds the relationship between brain size and manipulation complexity (Supplementary Table S6). Foraging group size of each species was used as a proxy for social complexity. The relationship between brain size and manipulation complexity persists even after controlling for foraging group size. Our results are therefore broadly consistent with the idea that social factors such as group size may not be the only important feature of primate brain size evolution; selection on ecological factors such as foraging skills may have been important too (Parker and Gibson, 1977; Byrne, 1997; Barton, 2012). However, the outcomes of the present study do not rule out some influence of social factors, as among primates the developmental acquisition of all complex manipulative skills has a major social-learning component (van Schaik and Pradhan, 2003), which could well be affected by group size and composition, as well as the degree of social tolerance.

Regarding this analysis, we must caution this sample is not optimal to identify the variables affecting brain size variation in primates. The aim of the current study was not to conduct such an analysis.

We therefore do not claim that variation in manipulation complexity is the sole or most important variable influencing brain size evolution.

Table S6. PGLS models with brain size as response variable, manipulation complexity as explanatory variables and foraging group size as potential confounding effect (*n* = 37, *Homo sapiens* included). Including body mass as covariate.

***P*-value model**	**λ**	**adj. r^2**	**predictor variables**	**estimate**	**std. error**	***P*-value**
			manipulation complexity	0.137	0.057	**0.022**
<0.001	0.111	0.928	log body	0.719	0.046	**<0.001**
			log foraging group size	0.053	0.044	0.235

Significant effects are highlighted in bold face.

Results of an alternative coding scheme of diet categories related to demands on manipulative skills

To investigate whether the results reported in this study are robust with respect to different coding schemes of the influence of diet on manipulation complexity, we conducted analogous tests with diet categories related to demands on manipulative skills instead of continuous estimates of diet quality. The results of PGLS regression models using this scheme are reported in Supplementary Table S7. Although *P*-values vary slightly in comparison with Tables 2 and Supplementary Table S2, on the whole the results are very similar.

Table S7. PGLS models with manipulation complexity as response variable and brain size as explanatory variables, terrestriality and diet category as covariates singly and as combined models (*n* = 34, *Homo sapiens* excluded). Including body mass as covariate.

model	*P*-value model	λ	adj. r^2	AIC	ΔAIC	predictor variables	estimate	std. error	*P*-value
model 1	**<0.001**	0	0.745	**59.345**	-	log brain	1.354	0.376	**0.001**
						log body	−0.608	0.303	0.054
						terrestriality	0.900	0.319	**0.008**
						diet category	−0.362	0.206	0.090
model 2	**<0.001**	0	0.728	60.773	1.428	log brain	1.286	0.387	**0.002**
						log body	−0.551	0.312	0.087
						terrestriality	0.948	0.328	**0.007**
model 3	**<0.001**	0	0.686	65.609	6.264	log brain	1.353	0.418	**0.003**
						log body	−0.489	0.333	0.153
						diet category	−0.412	0.228	0.082
model 4	**<0.001**	0	0.663	67.105	7.760	log brain	1.274	0.430	**0.006**
						log body	−0.416	0.343	0.234
model 5	**<0.001**	0.147	0.567	68.498	9.153	terrestriality	0.863	0.374	**0.028**
						log body	0.439	0.098	**<0.001**
model 6	**<0.001**	0.243	0.483	71.436	12.091	diet category	−0.361	0.240	0.143
						log body	0.528	0.096	**<0.001**

Significant effects and best-fitting models are highlighted in bold face.

Results using an alternative phylogenetic tree

To investigate whether the results reported in this study are robust with respect to different tree phylogenies, we conducted analogous tests using the 10k trees phylogeny (Arnold et al., 2010). The results of PGLS regression models using this phylogeny are reported in Supplementary Table S8. The positive correlation between manipulation complexity and relative brain size remains unaffected by the type of phylogeny that is used which corroborates the stability of our results. Furthermore, also with the 10k trees phylogeny manipulation complexity is best explained by brain size and terrestriality.

Table S8. PGLS models with manipulation complexity as response variable and brain size as explanatory variables, terrestriality and diet quality as covariates singly and as combined models (*n* = 33, *Ateles fusciceps*, *Saguinus labiatus*, *Saguinus imperator* and *Homo sapiens* excluded). As *Callicebus cupreus* is not present in the 10k tree phylogeny but the only species of that genus in our analyses, we replaced it by a sister species (*Callicebus moloch*). Including body mass as covariate.

model	*P*-value model	λ	adj. r^2	AIC	ΔAIC	predictor variables	estimate	std. error	*P*-value
model 1	**<0.001**	0	0.760	**55.990**	-	log brain	1.342	0.370	**0.001**
						log body	−0.568	0.298	0.066
						terrestriality	0.948	0.328	**0.007**
model 2	**<0.001**	0	0.754	57.588	1.598	log brain	1.439	0.410	**0.002**
						log body	−0.655	0.336	0.061
						terrestriality	0.930	0.319	**0.007**
						log diet quality	−0.339	0.579	0.563
model 3	**<0.001**	0	0.694	63.119	7.129	log brain	1.330	0.418	**0.003**
						log body	−0.432	0.332	0.203
model 4	**<0.001**	0	0.690	64.330	8.340	log brain	1.486	0.460	**0.003**
						log body	−0.577	0.376	0.136
						log diet quality	−0.540	0.644	0.409
model 5	**<0.001**	0.155	0.570	65.590	9.600	terrestriality	0.869	0.369	**0.025**
						log body	0.454	0.100	**<0.001**
model 6	**<0.001**	0.237	0.446	71.079	15.089	log diet quality	−0.046	0.650	0.944
						log body	0.539	0.106	**<0.001**

Significant effects and best-fitting models are highlighted in bold face.

Statistical assumption checks for phylogenetic generalized least-squares

Based on the findings by Matthews et al. (2010), ordinal ranked data, such as manipulation complexity measured in this study, can be treated as pseudo-continuous for PGLS analyses. The following assumption checks of Phylogenetic generalized least squares, described by Mundry (2014), were tested:

- In order to reach evenly distributed residuals around zero, all continuous variables were log-transformed.
- Categorical predictors (terrestriality and diet category) did not have 'too rare levels' (each level was present at least five times).
- Absence of strong collinearity among the predictors.
- Homogeneity and normality of the distribution of the residuals (and the response) was visually inspected.

- Absence of influential cases: No severely influential outliers were detected.

Notes on the number of observation bouts

To investigate whether the results in this study are robust with respect to different number of bouts observed for each species, we conducted all tests with a sample reduced to a fixed number of the first 20 observation bouts per species. As the results were largely identical to the total sample reported here, the reduced sample results are not reported here. Furthermore, we investigated whether a minimum of 20 bouts per species is enough to see the potential of manipulation complexity per species. We did this by constructing so-called collector's (saturation) curves per species and examining after how many observation bouts the highest manipulation complexity category was reached (Supplementary Fig. S4). As the highest manipulation complexity category was reached within 20 bouts for most of the observed species for which we had observed 25 bouts or more (15 out of 17 species, except for *Mandrillus sphinx* and *Pithecia pithecia*), we conclude that our results are robust against changes in observation time.

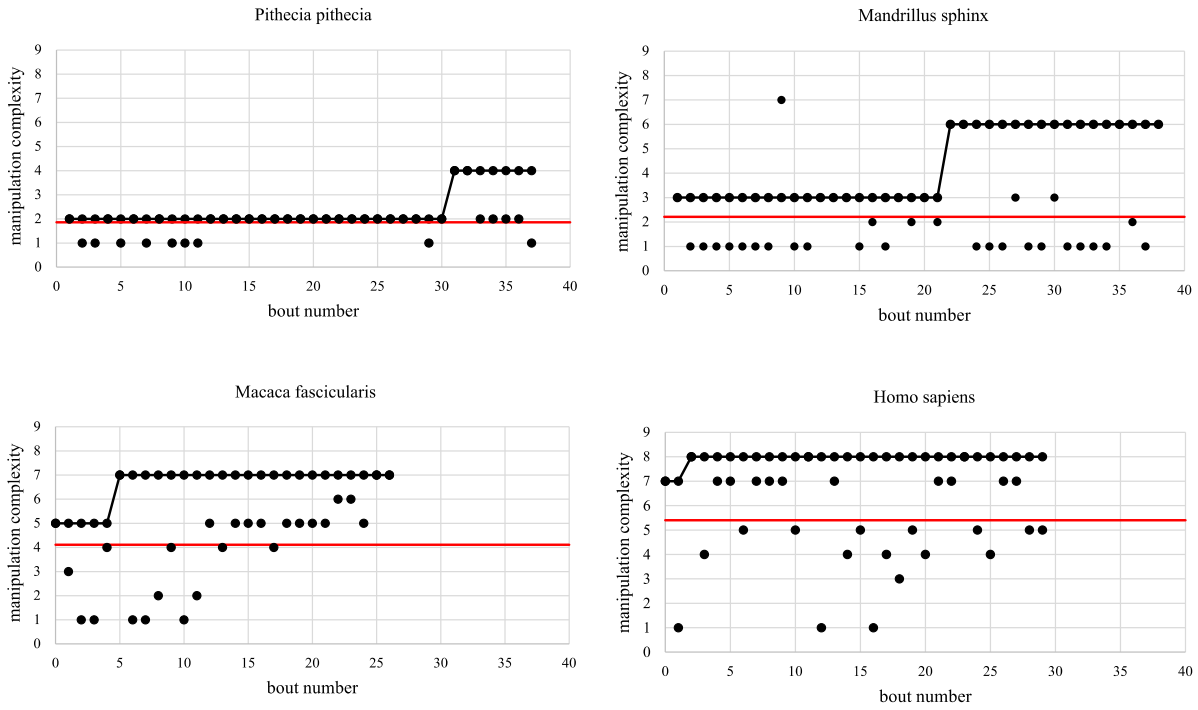

Figure S4. Saturation curves per species for examining after how many observation bouts the highest manipulation complexity category was reached. The red line indicates the mean manipulation complexity of a particular species.

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Dataset

List of species and data used for this study

Species	MC	Study site	# Bouts	# Ind.[$]	ECV [ml][¢]	BoM [g][¢]	Neocortex [g][@]	Cerebellum [g][@]	BoM brain parts [g] [@]	Terr.*	Diet quality	Diet category[&]	Tool use°	Extr. for.[§]	Cog. test[£]	Cog. test**	Group size
Ateles fusciceps	1.35	Parc Zool. et Bot. de Mulhouse	26	4	107.6	9160	-	-	-	0	-	-	0	0	1.28	-0.64	2.75
Ateles geoffroyi	2.48	Zoo Basel	21	7	103.5	7700	70.86	12.44	8000	0	434.2	1	0	0	1.28	-0.64	3.9
Callicebus cupreus	1.85	Zoo Basel	26	4	17.4	887	11.16	1.62	900	0	524.3	1	0	0	-	-	3.4
Callimico goeldii	1.43	Zoo Zurich	23	8	11.1	485	6.48	1.24	480	0	552.5	1	0	0	-	-	6.3
Callithrix geoffroyi	1.32	Zoo Zurich	22	7	9.8	338	4.37	0.78	280	0	541.2	0	0	1	-1.2	-0.86	7.5
Callithrix jacchus	1.33	University of Zurich	24	5	7.4	322	4.37	0.78	280	0	519.1	0	0	1	-1.2	-0.86	8.4
Cercocebus atys	2.24	Bioparco di Roma	21	5	85.9	6200	68.73	10.73	7900	1	439.7	1	0	0	0.25	-0.36	50
Cercopithecus diana	2.03	Parc Zool. et Bot. de Mulhouse	31	3/2	57.3	3900	47.55	6.29	4850	0	554.2	1	0	0	0.39	0.14	22
Cercopithecus hamlyni	3.84	Parc Zool. et Bot. de Mulhouse	25	5	51.2	2097	47.55	6.29	4850	0.5	605.2	0	0	0	0.39	0.14	8
Cercopithecus lhoesti	2.77	Parc Zool. et Bot. de Mulhouse	22	5	66.5	3450	47.55	6.29	4850	0.5	362.2	0	0	1	0.39	0.14	30

Species	MC	Study site	# Bouts	# Ind.[$]	ECV [ml][¢]	BoM [g][¢]	Neocortex [g][@]	Cerebellum [g][@]	BoM brain parts [g][@]	Terr.*	Diet quality	Diet category[&]	Tool use°	Extr. for.[§]	Cog. test[£]	Cog. test**	Group size
Colobus guereza	2.38	Toni's Zoo Rothenburg	21	3	72.6	7503	50.91	8.65	7000	0	348.3	0	0	0	-	-0.64	9.3
Eulemur coronatus	1.60	Parc Zool. et Bot. de Mulhouse	20	5	19.2	1422	12.21	3.33	1400	0	493.4	1	0	0	-0.5	-0.71	5.5
Eulemur macaco	1.23	Parc Zool. et Bot. de Mulhouse	22	2/2/2	22.7	1908	12.21	3.33	1400	0	453.6	1	0	0	-0.5	-0.71	8.5
Gorilla gorilla	5.00	Zoo Zurich	33	9	434.4	71500	341.44	69.25	105000	1	359.0	0	0	1	0.96	0.87	10.5
Hapalemur griseus	1.78	Parc Zool. et Bot. de Mulhouse	27	2/1	13.7	935	-	-	-	0	296.0	0	0	0	-	-	4.4
Homo sapiens	5.40	University of Zurich	30	12	1212.7	56700	1006.53	137.42	65000	1	690.6	1	1	1	-	-	37.7
Hylobates pileatus	2.14	Zoo Zurich	21	5/4	90.5	5440	65.8	12.08	5700	0	486.5	1	0	0	0.11	-0.79	4
Lemur catta	1.48	Zoo Basel	21	4	23.4	2210	10.69	2.59	-	0.5	527.6	1	0	0	-0.8	-0.79	14
Leontopithecus chrysomelas	1.63	University of Zurich	30	6	11.8	655	-	-	-	0.5	489.8	1	0	1	-	-1.36	4.75
Leontopithecus rosalia	1.20	Zoo Zurich	20	1	12.6	594.5	-	-	-	0	471.2	1	0	1	-	-1.36	5.4
Macaca fascicularis	4.11	Zoo Basel	27	17	61.0	3516	63.48	8.97	7800	0.5	432.4	1	1	1	0.55	1.64	27
Macaca sylvanus	3.76	Toni's Zoo Rothenburg	21	9	94.8	9625	63.48	8.97	7800	1	429.5	1	0	1	0.55	1.64	24
Macaca tonkeana	3.00	Parc Zool. et Bot. de Mulhouse	24	3	93.7	9000	63.48	8.97	7800	0.5	471.8	1	0	0	0.55	1.64	24

Species	MC	Study site	# Bouts	# Ind.[$]	ECV [ml][¢]	BoM [g][¢]	Neocortex [g][@]	Cerebellum [g][@]	BoM brain parts [g] [@]	Terr.*	Diet quality	Diet category[&]	Tool use°	Extr. for.[§]	Cog. test[£]	Cog. test**	Group size
Mandrillus sphinx	2.21	Bioparco di Roma	38	12	137.3	12800	95.75	8.74	-	1	482.2	1	0	0	0.43	-0.57	215
Pan troglodytes	4.38	Zoo Basel	26	10	391.6	33700	291.59	43.66	46000	0.5	491.5	1	1	1	1.66	2.80	5.6
Pithecia pithecia	1.86	Zoo Basel	37	7	31.6	1816	21.03	3.91	1500	0	479.9	1	0	0	-	-	4.4
Pongo abelii	3.89	Zoo Zurich	35	7	349.7	41151	200.26	97.80	73500	0	581.2	1	1	1	1.75	1.71	1.7
Propithecus verreauxi	1.44	Parc Zool. et Bot. de Mulhouse	27	1/1	26.1	3250	13.17	3.96	3480	0	318.8	0	0	0	-	-1.00	5.5
Saguinus bicolor	1.00	Parc Zool. et Bot. de Mulhouse	21	2/2/5	9.5	473	5.89	0.98	380	0	500.0	1	0	0	-	0.43	4.9
Saguinus imperator	1.62	Zoo Zurich	21	2	10.7	446	5.89	0.98	380	0	-	-	0	1	-	0.43	4
Saguinus labiatus	2.27	Zoo Basel	22	2	10.0	520	5.89	0.98	380	0	493.0	1	0	0	-	0.43	5
Saguinus oedipus	1.70	Zoo Basel	37	4	9.7	427	5.89	0.98	380	0	684.4	1	0	0	-	0.43	5.6
Saimiri sciureus	1.94	University of Zurich	31	7	23.5	821	15.54	2.26	660	0	435.4	1	0	1	-0.9	-0.79	45
Sapajus apella	2.54	Zoo Zurich	41	6	64.2	2501	46.43	7.87	3100	0	543.0	1	1	1	0.19	1.43	13.9
Symphalangus syndactylus	3.08	Zoo Zurich	24	3	124.5	11295	-	-	-	0	432.0	0	0	0	-	-	3.6
Theropithecus gelada	4.17	Zoo Zurich	23	27	123.2	14171	-	-	-	1	313.2	0	0	0	-	-0.43	103.8

Species	MC	Study site	# Bouts	# Ind.[$]	ECV [ml][¢]	BoM [g][¢]	Neocortex [g][@]	Cerebellum [g][@]	BoM brain parts [g] [@]	Terr.*	Diet quality	Diet category[&]	Tool use°	Extr. for.[§]	Cog. test[£]	Cog. test**	Group size
Varecia rubra	1.33	Parc Zool. et Bot. de Mulhouse	21	4	29.4	3300	15.29	4.29	3000	0	454.0	1	0	0	-0.4	-	5.5

Notes:

MC = manipulation complexity means, ECV = female endocranial volume, BoM = female body mass,

Bouts = number of observation bouts, # Ind. = Number of individuals observed

[$]Multiple numbers of individuals indicate that several groups from the same species were observed.

[¢]All brain and body mass measurements were from Lonsdorf and Ross (2012) and van Woerden (2010; 2012) except the body mass for *Saguinus imperator* was taken from Rowe and Myers (2011).

[@]Neocortex and cerebellum size and associated body mass measurements were taken from (Bush and Allman, 2004; Rilling and Insel, 1999; Stephan et al., 1981).

*Terrestriality, 1 = terrestrial (>60%), 0.5 = semi-terrestrial (>20%), 0 = arboreal

[&]Diet category, 1 = fruits and insects, 0 = gum and leaves

°Tool use, 0 = non-tool using species, 1 = tool-using species

[§]Extractive foraging, 0 = non-extractive foraging species, 1 = extractive foraging species

[£]Cognitive test performance measured by Deaner at al. (2007)

**Cognitive test performance measured by Reader et al. (2011)

Chapter 3

Being fat and smart: A comparative analysis of the fat-brain trade-off in mammals

Sandra A. Heldstab, Carel P. van Schaik, and Karin Isler

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Abstract

Humans stand out among non-aquatic mammals by having both an extremely large brain and a relatively large amount of body fat. To understand the evolution of this human peculiarity we report a phylogenetic comparative study of 120 mammalian species, including 30 primates, using seasonal variation in adult body mass as a proxy of the tendency to store fat. Species that rely on storing fat to survive lean periods are expected to be less active because of higher costs of locomotion and have increased predation risk due to reduced agility. Because a fat-storage strategy reduces the net cognitive benefit of a large brain without reducing its cost, such species should be less likely to evolve a larger brain than non-fat-storing species. We therefore predict that the two strategies to buffer food shortages (storing body fat and cognitive flexibility) are compensatory, and therefore predict negative co-evolution between relative brain size and seasonal variation in body mass. This trade-off is expected to be stronger in predominantly arboreal species than in more terrestrial ones, as the cost of transporting additional adipose depots is higher for climbing than for horizontal locomotion. We did, indeed, find a significant negative correlation between brain size and coefficient of variation (CV) in body mass in both sexes for the subsample of arboreal species, both in all mammals and within primates. In predominantly terrestrial species, in contrast, this correlation was not significant. We therefore suggest that the adoption of habitually terrestrial locomotor habits, accompanied by a reduced reliance on climbing, has allowed for a primate of our body size the unique human combination of unusually large brains and unusually large adipose depots.

Keywords: locomotion costs, bipedalism, terrestriality, body fat, brain size, seasonality

Introduction

Brain size varies considerably among mammalian species of any given body size (e.g., Striedter, 2005), and humans are arguably the most encephalized species. Similarly, the relative amount of body fat shows considerable variation among mammals (Pitts and Bullard, 1968; Pond and Mattacks, 1985; Tyler and Blix, 1990; Navarrete et al., 2011), and humans have remarkably large fat stores. In healthy humans, the amount of body fat accounts for about 12-23% of total body weight in men and 24-34% in women (Norgan, 1994; Kyle et al., 2001; McArdle et al., 2014; Montagnese et al., 2014; Prado et al., 2014; Bowen et al., 2015). This high amount of stored fat is not entirely a product of modern, industrial lifestyles, since body fat in women is around 19-24% even in hunter-gatherers or subsistence cultures inhabiting harsh environments (Lawrence et al., 1987; Yamauchi et al., 2000; Sherry and Marlowe, 2007; Pontzer et al., 2012). Other anthropoid primates, including our closest-living relatives, chimpanzees and bonobos, have only about 1-10% of body mass as fat (Pond and Mattacks, 1987; Dittus, 2013; Zihlman and Bolter, 2015). Thus, humans exhibit not only unusually large brains, but also unusually large adipose depots for a primate of our body size.

Because adipose tissue is not preserved in fossils, we need broad phylogenetic comparisons over several lineages to compare extant species and examine evolutionary processes underlying this human peculiarity. Many mammals live in seasonal habitats, in which periods of food scarcity impose severe energetic constraints. To deal with the challenge of lean periods, mammals have evolved physiological and/or cognitive strategies. The first, physiological buffering, generally involves storing fat, and is accompanied by seasonally reduced activity and decreased metabolic rates (in extremis leading to hibernation or torpor) as well as seasonal breeding if the reproductive cycle can be completed in less than a year (e.g., Pond, 1998; Heldmaier et al., 2004; McNab, 2008; Schmid and Speakman, 2009). Fat storage also has fitness costs. These arise from the increased energetic costs of locomotion due to larger body weight (Browning et al., 2006; Ghiani et al., 2015 and see discussion in Supplementary Online Material [SOM]), but also from increased predation risk or decreased hunting success due to reduced agility and speed (Gosler et al., 1995; Dietz et al., 2007; Zamora-Camacho et al., 2014). In arboreal species, adaptations for agile locomotion and terminal branch feeding may impose additional constraints on the quantity of fat stores (Dittus, 2013).

The second strategy to survive lean periods is cognitive flexibility. The Cognitive Buffer hypothesis (Allman et al., 1993; Deaner et al., 2003; Sol, 2009) predicts that living in more seasonal habitats favours the evolution of relatively larger brains, because enhanced cognitive abilities and behavioural flexibility to cope with seasonal challenges yield a selective advantage.

This hypothesis is supported by a positive correlation between climatic variability and brain size in Neotropical parrots (Schuck-Paim et al., 2008). In addition, migrating bird species have smaller brains than non-migrating bird species (Winkler et al., 2004; Sol et al., 2005), which may reflect a cognitive buffer effect in the resident species (Sol et al., 2005) or a reduced selective advantage of enhanced cognitive performance in migratory species (Sol et al., 2010). In platyrrhine and catarrhine primates, van Woerden et al. (2014) found a positive relationship between relative brain size and the amount of buffering, defined as the difference between environmental (and thus potentially experienced) and (actually) experienced seasonality. This finding suggests that a large brain allows monkeys to keep their energy intake relatively constant, e.g., by finding or accessing hidden or protected food sources, despite environmental fluctuations in food availability.

However, the advantage of enhanced cognitive abilities provided by increased brain size (Deaner et al., 2007; Reader et al., 2011) comes at the expense of increased energy costs. Brain tissue is among the most metabolically expensive tissues in the body (Rolfe and Brown, 1997; Niven and Laughlin, 2008), and the costs of brain function cannot be reduced temporarily (Lukas and Campbell, 2000; Karasov et al., 2004; Bauchinger et al., 2005). Selection can only favour changes of traits that produce a net fitness benefit, i.e., if benefits exceed costs. The fitness reduction due to the increased energetic costs of brain tissue may outweigh any fitness increase due to cognitive buffering in larger-brained species, especially in extremely seasonal or unpredictable habitats (van Woerden et al., 2010; Weisbecker et al., 2015). In periods of starvation, the brain is sustained by metabolising fat involving ketone bodies (Owen et al., 1967; Hasselbalch et al., 1994; Zhang et al., 2013). This can be a successful strategy to survive seasonally lean periods (Knott, 1998; Harrison et al., 2010), but on balance it is metabolically less efficient. The detour through fat metabolism increases the average amount of energy intake needed per day (Sokoloff, 1973; Hawkins et al., 1986; Mitchell and Fukao, 2001).

The high energy costs of the cognitive flexibility strategy implies that there is a trade-off between buffering seasonally lean periods either passively by storing body fat (“physiological buffering”) or actively by increasing relative brain size, which provides cognitive flexibility to access hidden and highly nutritious food items (“cognitive buffering”). Thus, we expect that selection favours increased brain size only for species which are active throughout the year and hence benefit from using their larger brains continuously. On the other hand, species that rely mainly on body fat and reduced activity to survive lean periods are expected to exhibit relatively small brains. This trade-off should be expressed as negative co-evolution between brain size and fat storage. Navarrete et al. (2011) found a negative correlation between the amount of adipose deposits and brain size in a broad sample of dissected mammal species. However, for various reasons it is necessary to revisit this issue.

First, the negative correlation between dissected fat deposits and brain size was not predicted but found while testing another hypothesis. Second, for some species fat deposits were estimated from single or very few specimens. Third, in primates, Navarrete et al. (2011) could measure only abdominal adipose depots of captive individuals, casting doubt on their finding of an absence of a negative correlation between brain size and adipose depots in primates. For all these reasons, the predicted brain-fat trade-off should be reassessed with an independent sample.

The first aim of this paper is therefore to conduct a broad test of the brain-fat trade-off in mammals. We do so using a novel proxy for the tendency to store body fat: the seasonal variation of body mass within a year, measured as the coefficient of variation (CV) in body mass. The CV body mass is a more precise measure of the tendency to store body fat as it covers the whole year, in contrast to the body fat values obtained from cadavers that can only be assessed at a given point in time, which leaves the seasonal fluctuations unknown (Wells, 2010). Moreover, this measure is available for a larger number of individuals in wild-living mammals.

Our second aim is to investigate the effects of substrate use on the brain-fat trade-off. In many species, locomotor costs are a substantial fraction of total daily energy expenditure (Garland, 1983; Elliott et al., 2013), and transporting adipose depots is costly (Taylor et al., 1982; Garby et al., 1988; Ekelund et al., 2002; Peyrot et al., 2009). Thus, we would expect fewer arboreal or volant species to rely on fat storage than terrestrial or aquatic ones, because flying and climbing involve higher cost of transporting adipose depots than swimming or moving horizontally (Alexander, 2003; Hanna et al., 2008). Accordingly, we predict a stronger trade-off between brain size and the potential to store fat in arboreal or volant species than in terrestrial or aquatic ones. This provides a starting point to investigate whether a bipedal, terrestrial lifestyle allowed humans to evolve the unique combination of unusually large brains and relatively large adipose depots. This combination may have been crucial, because without our extra fat stores we might not have been able to maintain high physical activity alongside our extremely large brains (Pontzer et al., 2016a; Pontzer et al., 2016b).

Material and methods

CV body mass as a proxy for the tendency to store body fat

In humans, approximately 75% of intra-individual variability in body weight of adult women can be attributed to fat storage in adipose depots (Webster et al., 1984). Similarly, in non-human mammals body fat explained between 41 and 92% of the intraspecific variation in body mass (Artiodactyla: 68-91% [Adamczewski et al., 1987; Adamczewski et al., 1995; Stephenson et al., 1998]; Carnivora: 41-79% [Beck et al., 2003; Crocker et al., 2012; Hilderbrand et al., 2000; Worthy et al., 1992]; Primates: 85-94% [Colman et al., 1999; Power et al., 2001]; Rodentia: 45-70% [Bintz and Strand, 1983; Galster and Morrison, 1976; Lidicker and Ostfeld, 1991; Pulawa and Florant 2000]). Several studies of mammals and birds found that the amount of body fat was highly correlated with carcass weight for each age and sex and hence that body weight was a good predictor of total body fat (Tribe and Peel, 1963; Bryden, 1969; Morton and Tung, 1971; Schaefer et al., 1976; Reimers et al., 1982; Serie and Sharp, 1989; Lidicker and Ostfeld, 1991; Drew, 1992; Dunbrack and Ramsay, 1993). Although fluctuations in the size of other organs such as liver, kidney or spleen can also affect seasonal changes in body mass, these effects are absolutely and relatively small (Mitchell et al., 1976; Bintz and Strand, 1983; Adamczewski et al., 1987; Gerhart et al., 1996; Campbell and MacArthur, 1998; Weber and Thompson, 1998) and often out of phase with cycles in body weight (Dauphine, 1975; Mitchell et al., 1976). We therefore used seasonal changes of body mass over a year as a proxy for the tendency to store body fat. We assume that these seasonal changes in body mass match food intake, and hence experienced seasonality, but not necessarily environmental seasonality (van Woerden et al., 2012; van Woerden et al., 2014). For a given species, we calculated the coefficient of variation (CV = standard deviation/mean) over monthly means of body mass for each sex separately. Data on CV body mass were found for a total of 120 mammalian species, including 111 species in the female dataset and 110 species in the male dataset. The complete datasets are given in the SOM.

Monthly body mass data were compiled from studies that reported adult body mass across the year. If several sources were available for one species, preference was given to studies on large sample sizes conducted in the wild. As captivity might affect body mass variation (under good husbandry conditions most animals gain weight in captivity; Leigh (1994)), we added provenience (wild/captivity) as a covariate in all analyses. Ideally, we would have preferred to use only studies from the wild that report mean body mass for 12 consecutive months. However, in contrast to studies in captivity, most body mass data of wild-living mammals have been recorded less frequently. To consider potential effects of unequal sampling we included the number of months sampled as a covariate in all analyses, and did not include studies with less than four months sampled.

If body mass data were given for four seasons, pooled across several months (e.g., spring, summer, autumn and winter), we set the number of months sampled to four (15 studies). In most species, monthly mean body mass data was distributed evenly across the year, except for *Antechinus stuartii*, *Myotis lucifugus*, *Rattus fuscipes*, *Zapus hudsonicus* and *Spermophilus franklinii*. We found no differences in the results when controlling for these potentially confounding variables (results shown in the SOM Tables S1-S3).

We also controlled for another possible confounding variable, pregnancy and lactation. Some studies include data from pregnant and lactating females in mean female body mass, which may artificially increase body mass variation in seasonal breeders. Obviously, pregnancy affects a female's weight due to the added weight of the offspring and associated tissues and fluids. Moreover, several studies also showed that females accumulate adipose depots before or during pregnancy and lactation (Randolph et al., 1977; Weiner, 1987; Hickling, 1991; Dufour and Sauther, 2002; Lassek and Gaulin, 2006). To control for this effect, we added the presence or absence of pregnant and/or lactating females in the study species as a covariate in all analyses. Furthermore, we analysed the subsample of studies including only non-pregnant and non-lactating females separately.

In some species, males store body fat for other purposes than to buffer lean periods, e.g., to have an advantage in male-male competition (Boinski, 1988; Lidgard et al., 2005; Crocker et al., 2012). However, it is usually impossible to disentangle the various reasons for body fat storage, as reproductive seasons and experienced seasonality in food intake are generally interrelated (Batzli and Pitelka, 1971; Bronson, 1989; Tyler and Blix, 1990; Réale et al., 2003). Whatever the specific purpose of fat storage, we would always expect a brain-fat trade-off due to the energetic costs of both brains and adipose deposits. To validate the use of CV body mass as a proxy for variation in body fat, we tested whether monthly body mass correlated with percentage body fat in a subsample of studies that measured both for at least five months in the same specimens (n = 8 species for females and n = 4 species for males, see SOM).

Brain size

For 105 of the 120 species of the CV body mass dataset, sex-specific data on endocranial volume (ECV) was either compiled from the literature or measured from museum specimens. The ECVs of 330 complete adult crania (third molar present) from three American museums (American Museum of Natural History, New York; National Museum of Natural History, Washington, D.C.; Field Museum of Natural History, Chicago) were measured using glass beads.

To control for allometric effects of size, sex-specific mean body mass was included as a covariate in the analyses, taking the overall mean from the same specimens for which CV body mass was determined. Dealing with seasonality is an ecological challenge, and we have no a priori prediction on how sociality might affect the brain-fat relationship. Nevertheless, differences in sociality may act as a confounding variable that independently influences both brain size evolution and fat storage, yielding spurious results. We therefore integrated group size as a covariate in our models. However, group size never exerted a significant effect, and the akaike information criterion (AIC) of the models that included group size was always higher than in those excluding it (results not shown).

Substrate use

Data from published sources were used to assign each species to one of two substrate use categories, terrestrial (0) or arboreal (1), based on their main habit. Species were classified as terrestrial when they spend more than 50% of observation time on the ground. Data on substrate use were taken from the published literature (Meier, 1983; Gittleman, 1986; Myers et al., 2006; Rowe and Myers, 2011, see SOM). Volant and aquatic taxa (Chiroptera, Cetacea and Pinnipedia) were not analysed, since too few species were available to test them separately. Instead, we graphically examined whether aquatic species fit into the pattern observed in terrestrial clades (and volant into arboreal ones), since volant and aquatic mammals can be regarded as the most extreme cases with respect to the locomotor costs of adipose depots.

Statistical analyses

All statistical analyses were performed using JMP™ 10.0 (SAS Institute Inc, 1989-2016) and R3.1.3 (R Core Team, 2015). All continuous variables were log-transformed before analysis in order to yield normally distributed residuals. To test for an intraspecific relationship between CV body mass and percentage of body fat, nonparametric Spearman correlations were used. To assess the overall significance of the correlation between CV body mass and percentage body fat across species for males and females, we used a weighted z-transform test to combine all p-values across species using the “combine.test” function from the “survcomp” package (Haibe-Kains et al., 2008) in R3.1.3 as recommended in Whitlock (2005). For this test, we assigned a weighting value based on the number of months available for each species.

In the interspecific models, a strong phylogenetic signal in the data, i.e., lambda estimated to be close to one in all models, warranted the use of methods to control for phylogenetic non-independence (Pagel, 1999). Phylogenetic analyses were performed in R, using phylogenetic generalized least squares regression (PGLS; Martins and Hansen (1997)) in the "caper" package (Orme et al., 2013). The phylogenetic tree was based on a composite supertree (Fritz et al., 2009) and is given in SOM Fig. S1. The outcome of PGLS can be strongly influenced by outliers or data points with a high leverage (Jones and Purvis, 1997). We therefore repeated all analyses after removing one data point with an absolute studentised residual larger than three (*Meles meles* in the female dataset). However, results were qualitatively very similar, and thus we only report results from analyses including all species. The CV body mass was treated as an independent variable and brain size as a dependent variable in the PGLS models, while mean body mass was included as a covariate. We also tested for an interaction effect between mean body mass and CV body mass, and potentially confounding variables as described above (SOM Table S4). All models were run for each sex-specific dataset separately and additionally in a subsample of non-pregnant and non-lactating females. Primates were also analysed separately, specifically to examine the questions raised by Navarrete et al's (2011) results for this order. To test the influence of locomotor costs on the brain-fat trade-off, the category of substrate use was included as an independent variable in the models. Furthermore, the influence of substrate use on CV body mass was also tested separately. To illustrate our findings, species or suborder mean values and residuals from non-phylogenetic least square regressions are shown in all figures (Figs. 1-2 and SOM Figs. S3-S4), following common practice (Symonds and Blomberg, 2014).

Results

CV body mass as a proxy for the tendency to store body fat

First, we validated the use of CV body mass as a proxy for the tendency to store body fat in a sample of species for which both measures were collected on the same individuals. In females, we found strong positive correlations between CV monthly body mass and percentage body fat in five out of eight species, and a positive trend for two additional species (SOM Fig. S2). Only one species (*Macaca fuscata*) did not exhibit any positive relationship. However, the body fat values of *M. fuscata* were based on only dissected mesenteric and omental fat (Muroyama et al., 2006). The Fisher's combined probability test revealed a significant overall positive correlation between CV body mass and percentage body fat ($p < 0.001$). In females, CV body mass may therefore be a reasonably good proxy for the tendency to store body fat.

In males, only one out of four species showed a significant relationship between CV monthly body mass and percentage body fat (SOM Fig. S2). Although the Fisher's combined probability test revealed a significant positive correlation between CV body mass and percentage body fat (p = 0.018), this test is asymmetrically sensitive to small p-values compared to large ones (Rice, 1990). We therefore include the analyses of the male dataset in the remainder of this paper, but placed stronger confidence in the interpretation of the results on females.

Influence of substrate use on the relationship between brain size and CV body mass

We had predicted that a brain-fat trade-off, and thus the negative correlation between brain size and CV body mass, would be more pronounced in predominantly arboreal species than in species with a largely terrestrial substrate use. Including substrate use as an effect in multiple regressions, we found a significant interaction effect between CV body mass and substrate use in females and a strong trend in males (Table 1 and Fig. 1) in the predicted direction. For the subsample of predominantly arboreal species, we found a significant negative correlation between brain size and CV body mass in both sexes, both in mammals in general and within primates (Table 2 and SOM Fig. S3). For the subsample of mostly terrestrial species, the correlation between brain size and CV body mass was not significant in either sex (Table 3). An analysis of the brain-fat relationship within terrestrial primates was not possible because our study comprised only two predominantly terrestrial primate species. In all subsamples, the brain-fat trade-off was always stronger in females compared to males and even stronger in the subsamples comprising only non-pregnant and non-lactating females (Tables 1-3). Overall, arboreal mammals exhibited less seasonal variation in body mass than did terrestrial species (Fig. 2 and SOM Table S5). The same difference was also observed within primates (Fig. 2 and SOM Table S5). The few data points available for aquatic species fit into the pattern observed for terrestrial clades, and the volants into that observed for arboreals, consistent with the prediction of a trade-off between brain size and the tendency to store body fat in volant clades, but not in aquatic ones (SOM Fig. S4).

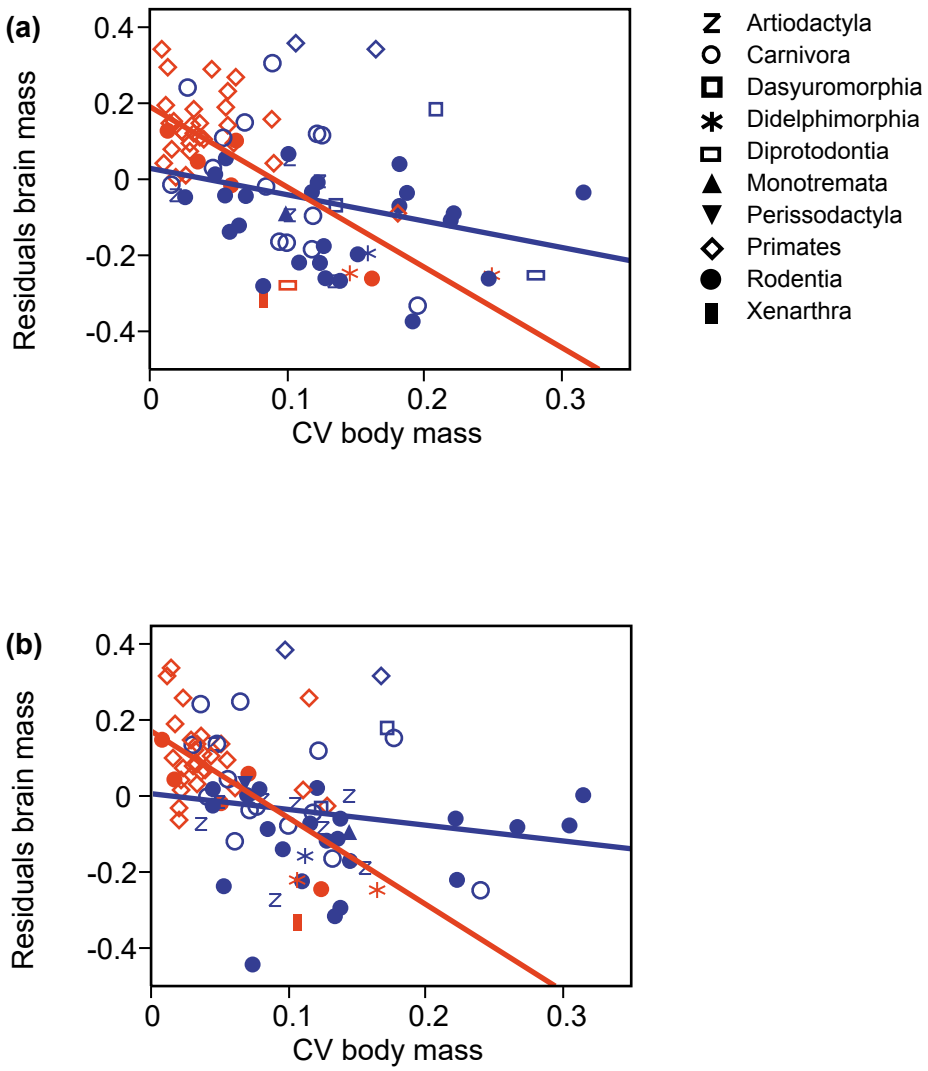

Figure 1. Relationship between log (brain size) and CV body mass in (**a**) males and (**b**) females, for the two types of substrate use (raw species values, blue = terrestrial, red = arboreal). Phylogenetically controlled statistics summarized in Tables 1-3.

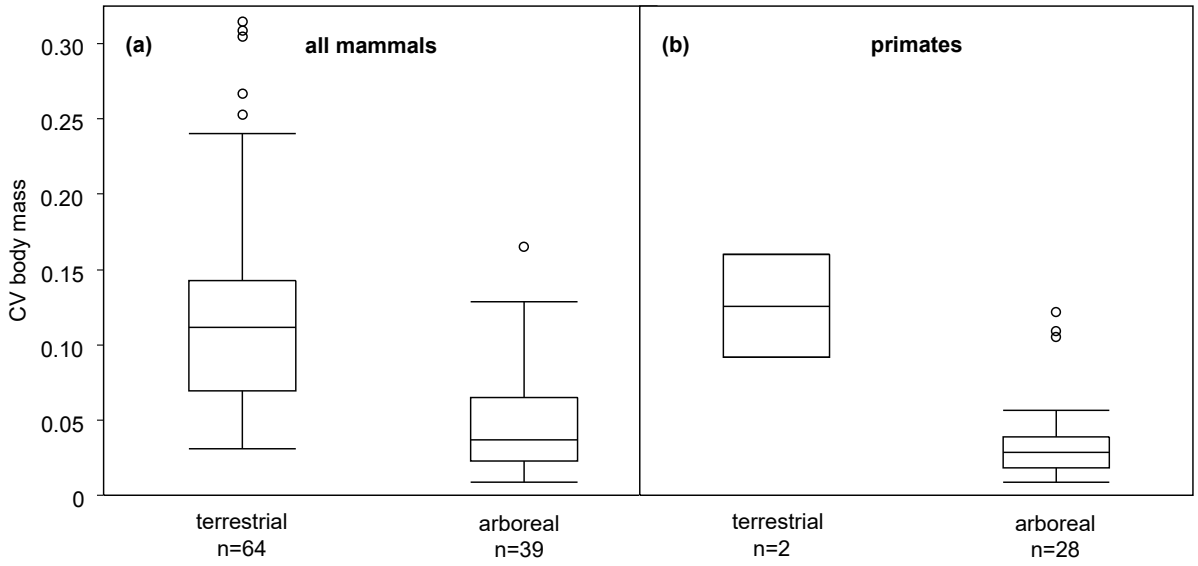

Figure 2. Coefficient of variation in body mass in (**a**) terrestrial and arboreal female mammals and (**b**) terrestrial versus arboreal female primates. For statistics, see SOM Table S5.

Table 1. Multiple regressions with log (brain size) as the dependent variable and CV body mass, log (mean body mass), substrate use, and the interaction between CV body mass and substrate use as independent variables (*n* = 88 for males, *n* = 89 for females).[a]

model[b]	lambda	adj. r^2	predictor variables	estimate	std. error	*p*-value
All mammals, males	0.899	0.901	CV body mass	-0.003	0.593	0.997
			log(mean body mass)	0.657	0.023	**<0.001**
			substrate use	0.181	0.190	0.344
			CV body mass*substrate use	−2.301	1.186	0.056
All mammals, all females	0.950	0.899	CV body mass	0.449	0.453	0.325
			log(mean body mass)	0.651	0.023	**<0.001**
			substrate use	0.174	0.200	0.389
			CV body mass* substrate use	−2.902	1.455	**0.049**
			inclusion of reproductive females in the study	-0.017	0.084	0.836

[a] Pinnipedia, Chiroptera and Cetacea are not included in the analyses.

[b]The *p*-values of both models were <0.001. Significant effects are highlighted in bold.

Table 2. Phylogenetic generalized least squares regression models[a] with log (brain size) as the response variable in arboreal mammals.

sample	*n*	lambda	adj. r^2	predictor variables	estimate	std. error	*p*-value
Arboreal mammals, males	37	0.918	0.867	CV body mass	-2.726	0.910	**0.005**
				log(mean body mass)	0.615	0.041	**<0.001**
Arboreal mammals, all females	36	0.986	0.853	CV body mass	-2.903	1.076	**0.011**
				log(mean body mass)	0.577	0.041	**<0.001**
				inclusion of reproductive females in the study	-0.097	0.085	0.262
Arboreal mammals, non-pregnant & non-lactating females	28	0.969	0.890	CV body mass	-3.528	1.126	**0.004**
				log(mean body mass)	0.592	0.044	**<0.001**
Arboreal primates, males	28	0.490	0.924	CV body mass	-3.067	1.160	**0.014**
				log(mean body mass)	0.667	0.042	**<0.001**
Arboreal primates, all females	28	1.000	0.897	CV body mass	-4.185	1.466	**0.009**
				log(mean body mass)	0.585	0.046	**<0.001**
				inclusion of reproductive females in the study	-0.293	0.086	**0.002**
Arboreal primates, non-pregnant & non-lactating females	25	1.000	0.899	CV body mass	-3.878	1.536	**0.019**
				log(mean body mass)	0.605	0.050	**<0.001**

[a]The *p*-values of all models were <0.001. Significant effects are highlighted in bold.

Table 3. Phylogenetic generalized least squares regression models[a] with log (brain size) as the response variable in terrestrial mammals.

sample	*n*	lambda	adj. r^2	predictor variables	estimate	std. error	*p*-value
Terrestrial mammals, males	51	0.890	0.906	CV body mass	-0.045	0.693	0.948
				log(mean body mass)	0.667	0.030	**<0.001**
Terrestrial mammals, all females	53	0.925	0.911	CV body mass	-0.445	0.543	0.417
				log(mean body mass)	0.675	0.029	**<0.001**
				inclusion of reproductive females in the study	0.066	0.136	0.629
Terrestrial mammals, non-pregnant & non-lactating females	5	0	0.993	CV body mass	-0.130	5.435	0.983
				log(mean body mass)	0.808	0.063	**0.006**

[a]The *p*-values of all models were <0.001. Significant effects are highlighted in bold.

Discussion

Testing the brain-fat trade-off

Using seasonal body mass variation as a proxy for the tendency to store body fat, we found that brain size and the tendency to store body fat are negatively correlated in predominantly arboreal mammals. This result adds to other studies showing that seasonality plays a role in brain size evolution (Schuck-Paim et al., 2008; van Woerden et al., 2010; van Woerden et al., 2012; van Woerden et al., 2014; Weisbecker et al., 2015). It also lends support to our prediction that encephalization (cognitive buffering, active strategy of survival) and fat storage (physiological buffering, passive strategy of survival) are compensatory strategies to buffer against seasonal starvation, unless the reduced cost of transport of additional body fat, as in terrestrial species, alleviates this trade-off and thus allows organisms to combine both strategies.

We attempted to assess the validity of using CV body mass as a proxy for the variation in adipose depots. While significant positive correlations between body mass and percentage body fat were found for females in most species, for males a significant correlation was found in only one out of four species. Taking these results from the rather small samples at face value, this suggests that there is a sex-specific difference in body mass variation over the year, perhaps partly due to sexual selection. Female reproductive success relies more on the ability to store body fat, as it enables the female body to bear the energy costs of pregnancy and lactation (e.g., Bercovitch, 1987; Richard et al., 2000; Ellison, 2001; Dufour and Sauther, 2002; Zenuto et al., 2002; Martin, 2007). These studies and our finding that the brain-fat trade-off was more pronounced in females than in males make it reasonable to conclude that in females energetic constraints on reproduction aggravate the trade-off between brain size and body fat. Males, on the other hand, may rely less on body fat to achieve increased reproductive success (Leader-Williams and Ricketts, 1982; Setchell and Dixson, 2001), but rather on muscle mass, as robust musculature would aid in mate searching and be advantageous during male-male fights. This sex difference can explain the relatively lower strength of the correlation of body mass with body fat over the year in males (Bonnet et al., 1998; Schulte-Hostedde et al., 2001; Boos et al., 2002).

These conclusions must remain somewhat preliminary, especially for males, in the absence of a more thorough validation study of CV body mass as a proxy of variation in body fat. In any case, the use of dissected body fat is also far from ideal, as body fat values obtained only from cadavers reflect the values at the time of death, and seasonal fluctuations therefore remain unknown (Wells, 2010). It would evidently be very useful if not only body mass variation but also a more direct measure of body fat content could be assessed in a large number of wild animals.

Although the published literature contains a variety of measures of adipose depots in living subjects such as palpation, skinfold thickness, perirenal adiposity, the number of adipocytes in bone marrow, and adipocyte volumes from tissue samples (Ellis, 2000), these measures have not yet been compared to each other or across species. This assessment would therefore require targeted studies.

Effects of substrate use

Adipose depots contribute both to body mass, which increases the total energy requirement for physical activity, and to body volume, which may impact locomotor traits such as speed and agility. Several lines of evidence in our study suggest that substrate use affects these costs of body fat through the latter's effects on locomotion efficiency (see SOM for an extensive discussion). First, we found a stronger trade-off between brain size and the potential to store body fat (as proxied by CV body mass) in arboreal clades compared to terrestrial ones. Several studies showed that climbing and other locomotor types used in arboreal niches, such as vertical clinging and leaping, involve much higher costs of transporting additional weight than moving horizontally (Warren and Crompton, 1998; Hanna et al., 2008). Thus, if locomotion costs are higher, less energy can then be allocated to the brain, as postulated by the expensive brain framework (Isler and van Schaik, 2009), resulting in a stronger brain-fat trade-off in arboreal species compared to terrestrial ones.

Second, we showed that arboreal species exhibited less seasonal variation in body mass than terrestrial mammals, potentially suggesting that arboreal species face constraints on the amount of body fat they can store. However, our sample of arboreal mammals is heavily biased towards primates, as body mass data of more arboreal non-primate mammals are presently lacking. Future studies testing the relationship between body fat and substrate use are therefore needed to substantiate this finding.

Third, in fully aquatic species, large body size and volume do not increase cost of transport if geometric similarity of the body form is maintained (Marino, 1998; Pond, 1998; Alexander, 2003). Indeed, rather than hamper, fat stores enhance locomotor efficiency, which has been demonstrated in several seal species (Beck et al., 2003; Adachi et al., 2014; Richard et al., 2014). It seems likely, therefore, that an aquatic lifestyle does not entail a brain-fat trade-off, allowing the combination of both strategies of fat storage and brain enlargement to buffer seasonally lean periods. Indeed, several marine or semi-aquatic mammals, such as whales and dolphins, seals, sea lions and beavers, exhibit both a relatively large brain and large adipose depots compared to other mammals (Marino, 1998; Pond, 1998), perhaps also due to thermoregulatory needs (Mclellan et al., 2002; Montie et al., 2008; Zeng et al., 2015).

Due to the small number of aquatic species in our sample (three pinniped species and the bottle-nosed dolphin *Tursiops truncatus*), our data are inconclusive in this respect. Moreover, CV body mass may not be an adequate proxy of the tendency to store body fat in fully aquatic species, as they probably maintain a high level of body fat throughout the year.

Fourth, we predicted (but could not test) that flying species experience an even stronger trade-off between brain size and body fat than other animals. Flying mammals, such as bats, are expected to have even higher costs of transporting adipose depots compared to terrestrial and arboreal clades. It is difficult to test this hypothesis using a comparative approach, as there is only one phylogenetic group of volant mammals, but, not surprisingly, the proportion of body fat in bats indeed tends to be relatively low, regardless of their size (Wells, 2010). For birds, we would expect that the relationships between brain size and fat storage also depend on their mode of flight or their locomotor habits. Migrating birds or lineages that depend on flapping flight are expected to show a stronger trade-off than non-migrating birds or lineages that evolved energy-efficient forms of flight such as soaring. In sum, our study confirms the hypothesis that the trade-off between brain size and the potential to store fat is stronger in arboreal clades compared to terrestrial ones. Whether it can be expanded to volant and aquatic animals requires further testing.

Implications for hominin evolution

Humans stand out among non-aquatic mammals by having both an extremely large brain and a high amount of body fat (Wells, 2010). Our comparative results therefore provide support for the notion that, among species with a more terrestrial lifestyle, the brain-fat trade-off is relaxed relative to arboreal ones because of the lower costs of transporting additional adipose tissue. We admit that extending the conclusions from such a comparative study to explain the evolutionary trajectory of a single lineage is risky, especially in the light of the small number of predominantly terrestrial primate species in our study (*Pan troglodytes* and *M. fuscata*). Nevertheless, in our dataset these two species were among the primates with the highest CV body mass values. A recent study reporting estimates of body fat percentage using the doubly-labelled water method (Pontzer et al., 2016a) found similar relationships within hominoids. The genus *Pan*, which most frequently engages in vertical climbing and has the longest daily travel distances amongst great apes, exhibited a lower proportion of body fat than both *Gorilla* and *Pongo*, which showed similar values. Gorillas are relatively terrestrial and their daily travel distances are very short, suggesting that low locomotion costs relax the constraints on the quantity of fat stores.

As wild orangutans are largely arboreal (Ashbury et al., 2015), it remains unclear whether the high percentage of body fat noted in the Pontzer et al. (2016a) study is due to a captivity effect or whether the capacity of fat storage is strongly selected for in this genus, which suffers from severe and unpredictable starvation periods due to El Niño effects (Knott, 1998). Preliminary data on brain size support the notion that female *Pongo pygmaeus morio*, the subspecies affected most by habitat unpredictability, exhibit smaller brains than the other subspecies or *Pongo abelii* (Taylor and van Schaik, 2007). However, reliable conclusions about the interrelations between fat storage, brain size, and locomotor mode within hominoids require more detailed data on these traits in several wild ape species and subspecies.

Humans have adopted a fully terrestrial lifestyle and almost completely abandoned climbing, which is energetically very expensive (Pontzer and Wrangham, 2004; Hanna et al., 2008). In addition, early *Homo* also evolved an energetically more efficient striding gait compared to the probably less efficient australopithlike form of bipedalism (Bramble and Lieberman, 2004; Nagano et al., 2005; Pontzer et al., 2009; Pontzer et al., 2010). It is therefore likely that lowering the energy costs of locomotion early on in the evolution of *Homo* may have allowed for selection to favour 'diversion' of this energy to the brain. Besides this reallocation, the human lineage also evolved an acceleration in metabolic rate, i.e., a higher energy throughput and thus more energy for larger brains or increased production (Pontzer et al., 2016a). The combination of efficient walking, metabolic acceleration and several other factors (Aiello and Wheeler, 1995; Burkart et al., 2009; Wrangham, 2009; Isler and van Schaik, 2014) may therefore have enabled the extraordinary brain enlargement evident in our lineage. Moreover, abandoning climbing and adopting more efficient bipedalism may have reduced the load effect of adipose depots on the energy costs of locomotion. Navarrete et al. (2011) estimated that 10% additional fat stores would increase the percentage of energy used for locomotion by about 2-3% in chimpanzees, but by only 1% in extant human foragers. They assumed that the costs of locomotion increase less steeply with additional body mass in bipedal locomotion compared to quadrupedal locomotion, or in efficient bipedalism compared to australopith bipedalism; however, this remains to be tested.

Seasonality in diet composition or food availability accounts for much of the variability among mammalian species in brain size (van Woerden et al., 2014; Weisbecker et al., 2015) and average fatness (Pond, 1998). Habitat seasonality is also often suggested as a major selective factor in the hominin radiation (Foley, 1993; Burkart et al., 2009; Wrangham, 2009). Acceleration in metabolic rate in larger-brained early humans is likely to have aggravated the impact of seasonal fluctuations in energy intake, because increased energy throughput exposes humans to a greater likelihood of energy shortfalls (Pontzer et al., 2016a).

As brain tissue is among the most metabolically expensive tissues in the body (Rolfe and Brown, 1997; Niven and Laughlin, 2008), and the costs of brain function cannot be temporarily reduced (Lukas and Campbell, 2000; Karasov et al., 2004; Bauchinger et al., 2005), we propose that increased body fat deposits may have been essential in providing an energy buffer against temporal fluctuations in energy intake in early *Homo*. It seems likely, therefore, that the almost unique human strategy of combining cognitive buffering during lean periods (for example, by extractive foraging and tool use) with the increased potential to store fat in adipose depots (physiological buffering) was driven by pronounced seasonal variation in food sources, which was a characteristic of the African tropical savannah mosaic during the late Pliocene. This strategy in humans also enabled early *Homo* species to survive the unpredictability of new environments as they greatly expanded their geographic range (Wells and Stock, 2007; Wells, 2012). Under these conditions, freedom from arboreal constraints on the amount of body fat and the development of large brains may have helped the first terrestrial hominins to maintain an approximately constant energy supply despite the environmental uncertainty of resource availability in unfamiliar terrestrial habitats (Foley, 1987; Navarrete et al., 2011; Wells, 2012).

Acknowledgements

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Supplementary material

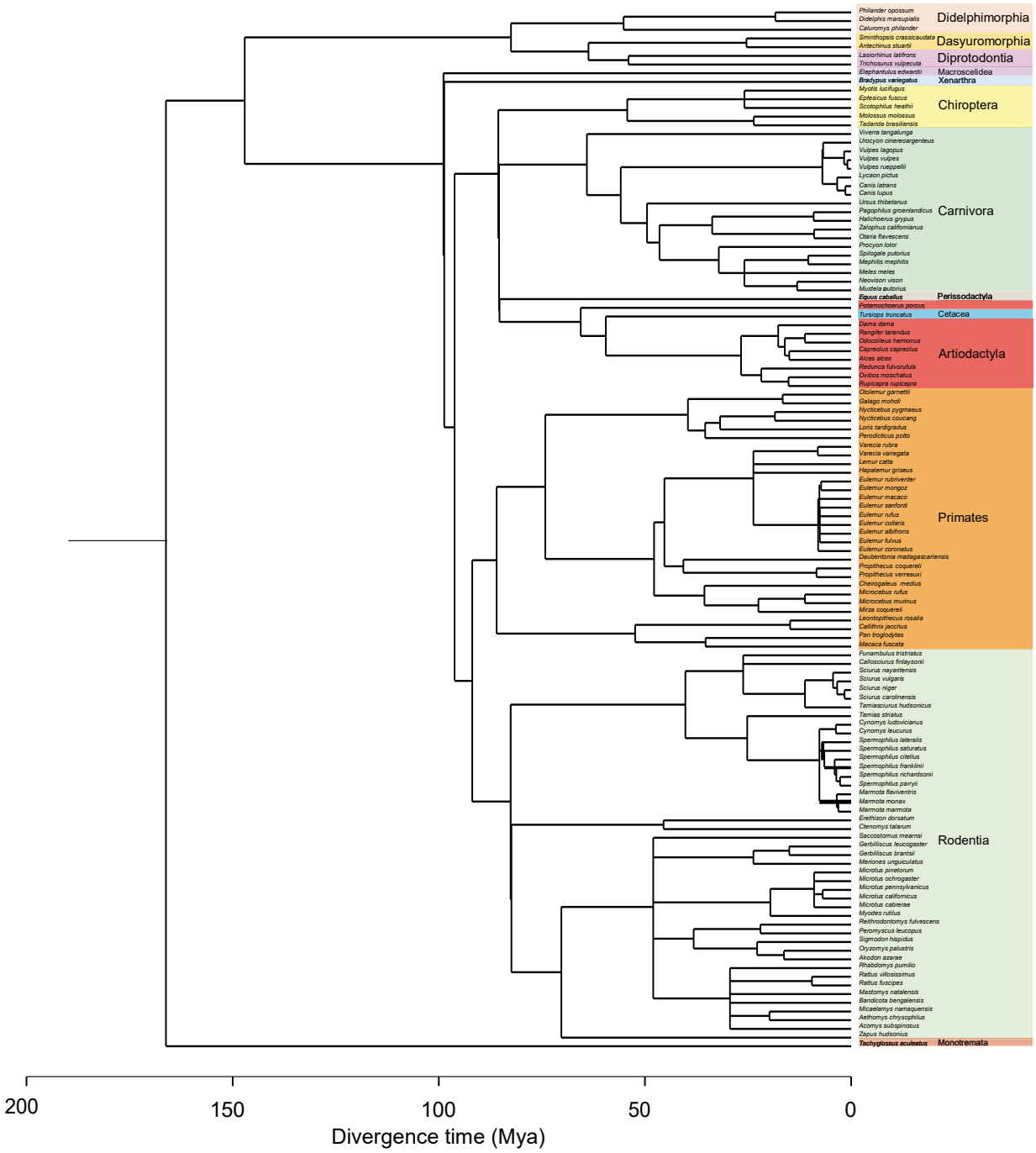
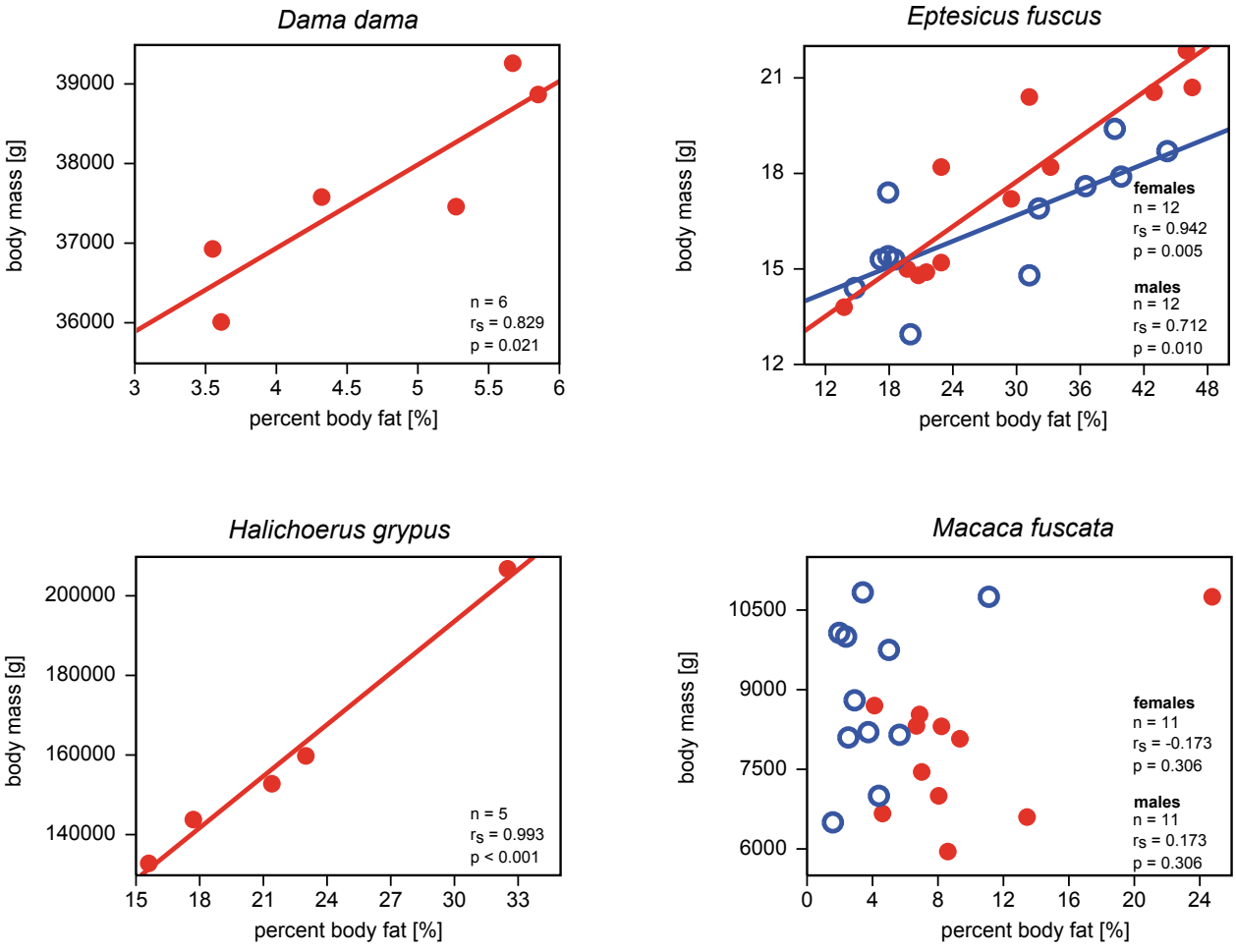


Figure S1: This phylogenetic tree of 120 mammal species based on Fritz et al. (2009) was used for the analyses reported in the main text. For details, see the methods section of the original paper.

Supplementary results

Results of the relationship between monthly body mass and monthly percent of body fat

We tested whether coefficient of variation (CV) body mass is a good proxy for the tendency to store body fat by correlating monthly body mass and monthly percentage of body mass made up by fat derived from the same individuals. In two species (*Macaca fuscata* and *Marmota monax*) only abdominal fat mass per month was available. In one species (*Microtus pinetorum*), dry weight instead of body mass was used to test for a relationship between body mass and percentage of body fat, as percentage of total body fat was based on dry weight of the carcasses (body fat values were obtained through ether extraction; (Lochmiller et al., 1983)). In females, monthly body mass was positively correlated with percentage of body fat in five out of eight species, supporting the use of CV body mass as a proxy of the tendency to store body fat. In males, CV body mass did not predict percentage of body fat very well, as in only one species out of four was a significant positive relationship between body mass and body fat found (Fig. S2).



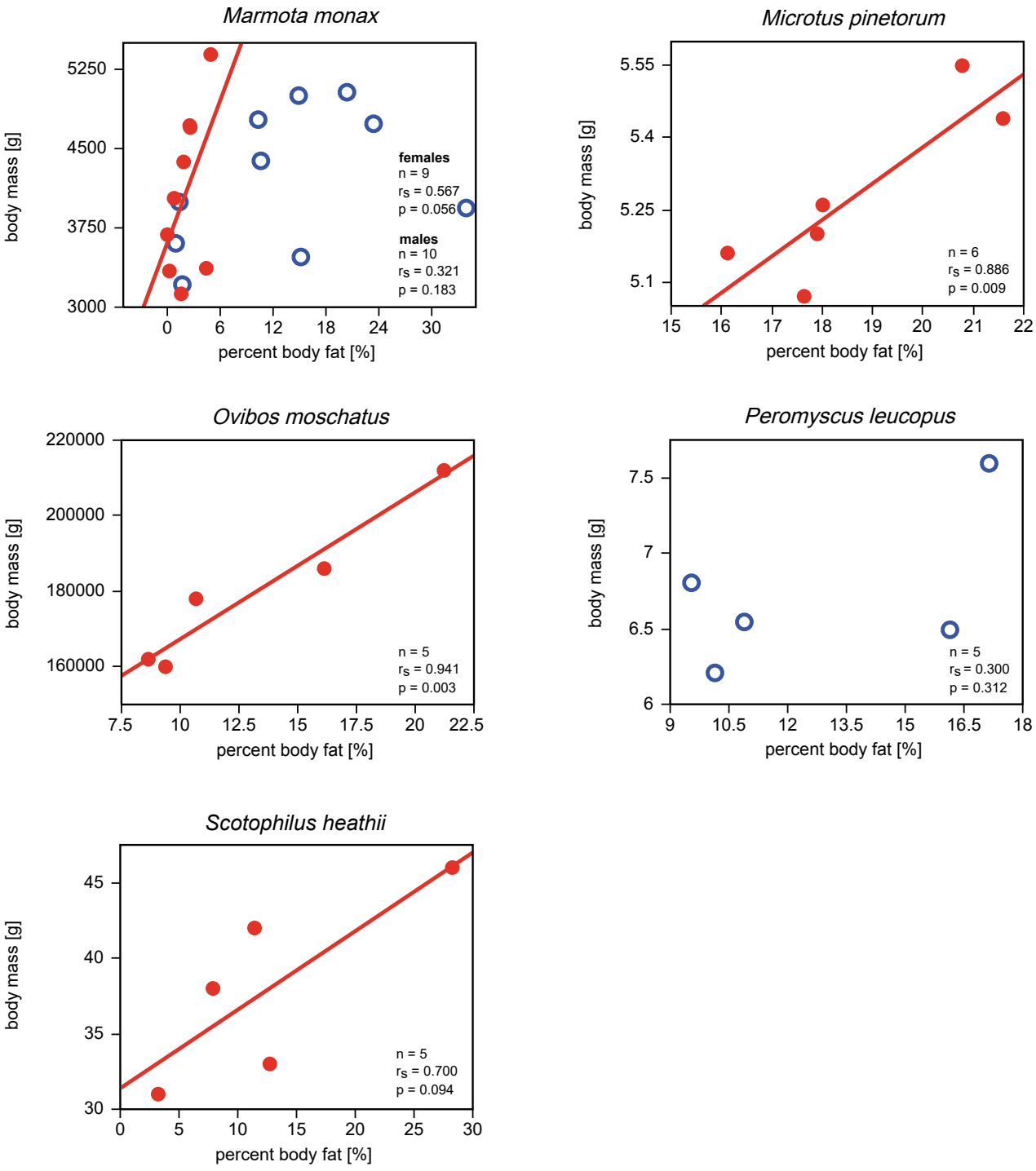


Figure S2. Monthly body mass versus percent of body fat within different mammalian species: Bivariate plots of the regression of monthly body mass versus percent body fat for males (open blue circles) and for female mammals (solid red circles). (Results of Spearman correlations in bottom right corner of each plot.)

Results of all analyses corrected for potentially confounding variables

To investigate whether the results reported in this study were robust with respect to possible confounding variables, we added provenience (wild = 1/captivity = 0) and the number of months sampled as covariates. As in the main text, we added the inclusion of reproductive females in the study (presence = 0 or absence = 1 of pregnant and/or lactating females in the study species) as a covariate in all analyses (Tables S1–S3).

Table S1. Multiple regressions with log(brain size) as the dependent variable and CV body mass, log(mean body mass), substrate use, and the interaction between CV body mass and substrate use as independent variables (*n* = 83 for males, *n* = 85 for females). Note that Pinnipedia, Chiroptera and Cetacea are not included in the analyses.

model	lambda	adj. r^2	predictor variables	estimate	std. error	*p*-value
All mammals, males	0.903	0.906	CV body mass	-0.091	0.633	0.886
			log(mean body mass)	0.656	0.023	**<0.001**
			substrate use	0.181	0.191	0.345
			CV body mass*substrate use	−2.370	1.191	**0.050**
			provenience	-0.032	0.074	0.670
			number of months	-0.016	0.011	0.140
All mammals, all females	0.954	0.904	CV body mass	0.501	0.464	0.283
			log(mean body mass)	0.652	0.024	**<0.001**
			substrate use	0.171	0.201	0.396
			CV body mass*substrate use	−2.825	1.444	**0.054**
			provenience	0.042	0.073	0.566
			number of months	-0.008	0.009	0.349
			inclusion of reproductive females in the study	0.014	1.444	0.879

The *p*-values of both models were <0.001. Significant effects and trends are highlighted in bold.

Table S2. Phylogenetic generalized least squares regression models with log (brain size) as the response variable in arboreal mammals.

sample	*n*	lambda	adj. r^2	predictor variables	estimate	std. error	*p*-value
Arboreal mammals, males	37	0.963	0.853	CV body mass	-2.602	0.974	**0.012**
				log(mean body mass)	0.617	0.044	**<0.001**
				provenience	0.043	0.099	0.667
				number of months	-0.026	0.027	0.344
Arboreal mammals, all females	36	0.986	0.851	CV body mass	-3.116	1.485	**0.044**
				log(mean body mass)	0.588	0.043	**<0.001**
				provenience	-0.181	0.337	0.595
				number of months	-0.030	0.033	0.371
				inclusion of reproductive females in the study	-0.210	0.277	0.454
Arboreal mammals, non-pregnant & non-lactating female	28	0.978	0.881	CV body mass	-2.692	1.818	0.152
				log(mean body mass)	0.589	0.053	**<0.001**
				provenience	0.397	0.489	0.426
				number of months	0.045	0.053	0.408

The *p*-values of all models were <0.001. Significant effects are highlighted in bold.

Table S3. Phylogenetic generalized least squares regression models with log (brain size) as the response variable in terrestrial mammals.

sample	*n*	lambda	adj. r^2	predictor variables	Estimate	std. error	*p*-value
Terrestrial mammals, males	46	0.903	0.911	CV body mass	-0.016	0.757	0.983
				log(mean body mass)	0.661	0.031	**<0.001**
				provenience	-0.105	0.109	0.341
				number of months	-0.019	0.013	0.171
Terrestrial mammals, all females	49	0.935	0.913	CV body mass	-0.545	0.585	0.356
				log(mean body mass)	0.671	0.030	**<0.001**
				provenience	0.026	0.096	0.784
				number of months	-0.007	0.011	0.532
				inclusion of reproductive females in the study	0.077	0.143	0.591

The *p*-values of all models were <0.001. Significant effects are highlighted in bold.

Results of the relationship between brain size and CV body mass including the interaction effect between CV body mass and body mass

Models including the interaction term between CV body mass and body mass show that the effect of this interaction is not statistically significant, neither in females nor in males (Table S4).

Table S4. Multiple regressions with log(brain size) as the dependent variable and CV body mass, log(mean body mass), and the interaction between CV body mass and log(mean body mass) as independent variables (*n* = 88 for males, *n* = 89 for females).

model	lambda	adj. r^2	predictor variables	estimate	std. error	*p*-value
All mammals, males	0.897	0.901	CV body mass	0.292	1.363	0.831
			log(mean body mass)	0.664	0.034	**<0.001**
			substrate use	0.176	0.192	0.362
			CV body mass*substrate use	-2.273	1.201	**0.062**
			CV body mass*log(mean body mass)	-0.050	0.205	0.807
All mammals, females	0.956	0.897	CV body mass	0.403	1.192	0.736
			log(mean body mass)	0.632	0.030	**<0.001**
			substrate use	0.178	0.203	0.381
			inclusion of reproductive females in the study	-0.020	0.084	0.808
			CV body mass*substrate use	-2.971	1.460	**0.045**
			CV body mass*log(mean body mass)	0.150	0.189	0.430

The *p*-values of both models were <0.001. Significant effects and trends are highlighted in bold.

Results of the influence of substrate use on CV body mass

On average, CV body mass is significantly higher in terrestrial species than in arboreal species (Table S5). The same is also true within primates as a group, although the number of mainly terrestrial primate species in our sample was only two. For graphical illustration and discussion, see the result and discussion section of the original paper.

Table S5. Phylogenetic generalized least squares regression models with CV body mass as the response variable.

model	*n*	lambda	adj. r^2	predictor variables	estimate	std. error	*p*-value
All mammals, males	102	0.367	0.078	substrate use	-0.055	0.018	**0.003**
All mammals, all females	103	0	0.266	substrate use	-0.044	0.016	**0.007**
				inclusion of reproductive females in the study	-0.039	0.016	**0.021**
All mammals, non-pregnant & non-lactating females	33	0	0.317	substrate use	-0.055	0.014	**<0.001**
Primates, males	30	0.803	0.119	substrate use	-0.090	0.040	**0.035**
Primates, all females	30	1.000	0.255	substrate use	-0.085	0.038	**0.034**
				inclusion of reproductive females in the study	-0.026	0.012	**0.045**

The *p*-values of all models were <0.015. Significant effects are highlighted in bold.

Results of the relationship between brain size and CV body mass in arboreal species

For the subsample of arboreal species, we found a significantly negative correlation between brain size and CV body mass in both sexes, both in mammals and within primates (Table 2 in the main text and SOM Fig. S3).

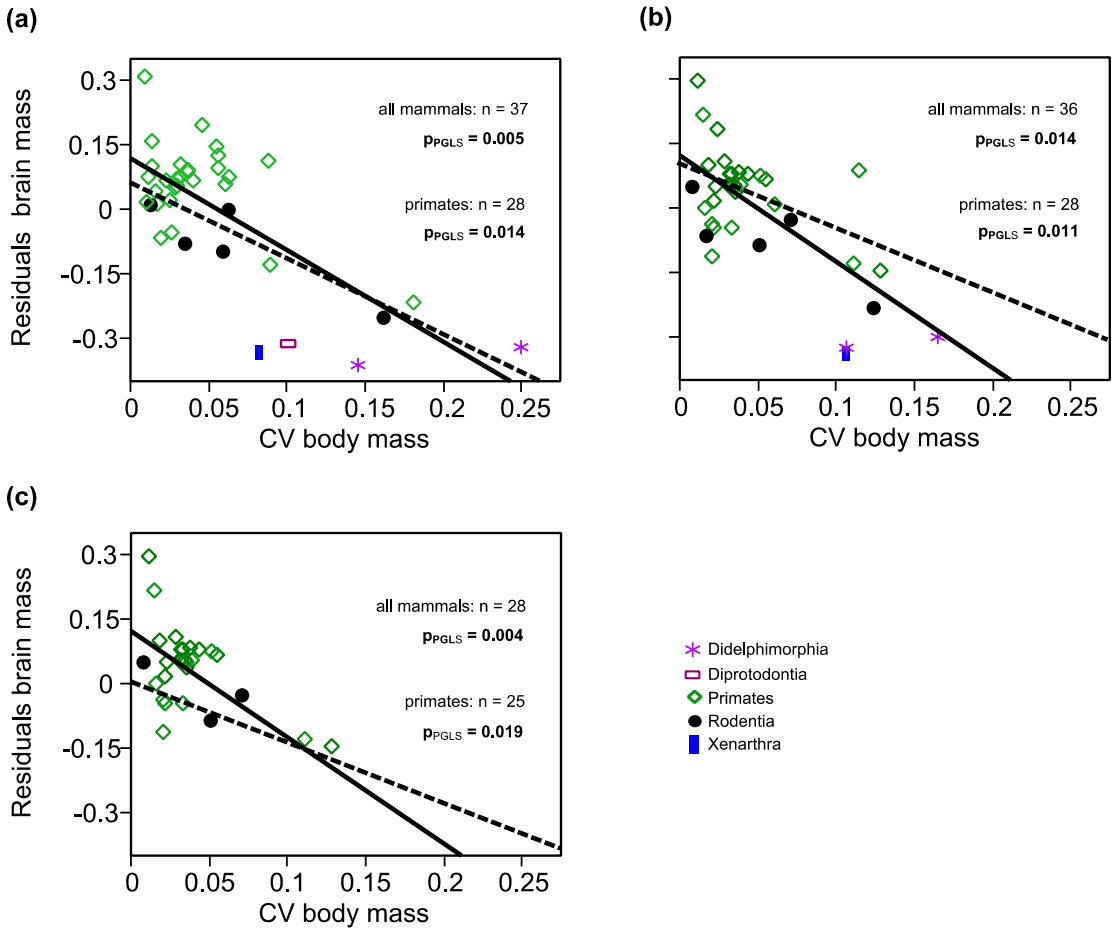


Figure S3. Brain size versus CV body mass in arboreal mammals and primates: Bivariate plots of the regression of the residuals of log(brain size) vs. log(body mass) versus CV body mass for males (**a**), females (**b**) and for the subsample of non-pregnant and non-lactating females (**c**) both for mammals (solid line) and for primates (dashed line) (raw species values). Details of phylogenetic models are shown in Table 2. Species values are listed in the SOM Dataset for females and for males.

Aquatic and volant species

From the graphical examination it seems that the aquatic species fit the general pattern of terrestrial species quite well (Fig. S4). As in terrestrial species, there are some aquatic species that combine a relatively large brain with a relatively large variation in body mass, and therefore a fat-brain trade-off is probably weak or absent.

The volant species fall within the stronger negative correlation between brain size and CV body mass observed for arboreal species (Fig. S4). Our finding is consistent with reports that relatively small-brained Chiroptera species store body fat to hibernate or migrate (Stephan and Nelson, 1981; Baron et al., 1996; McGuire and Ratcliffe, 2011).

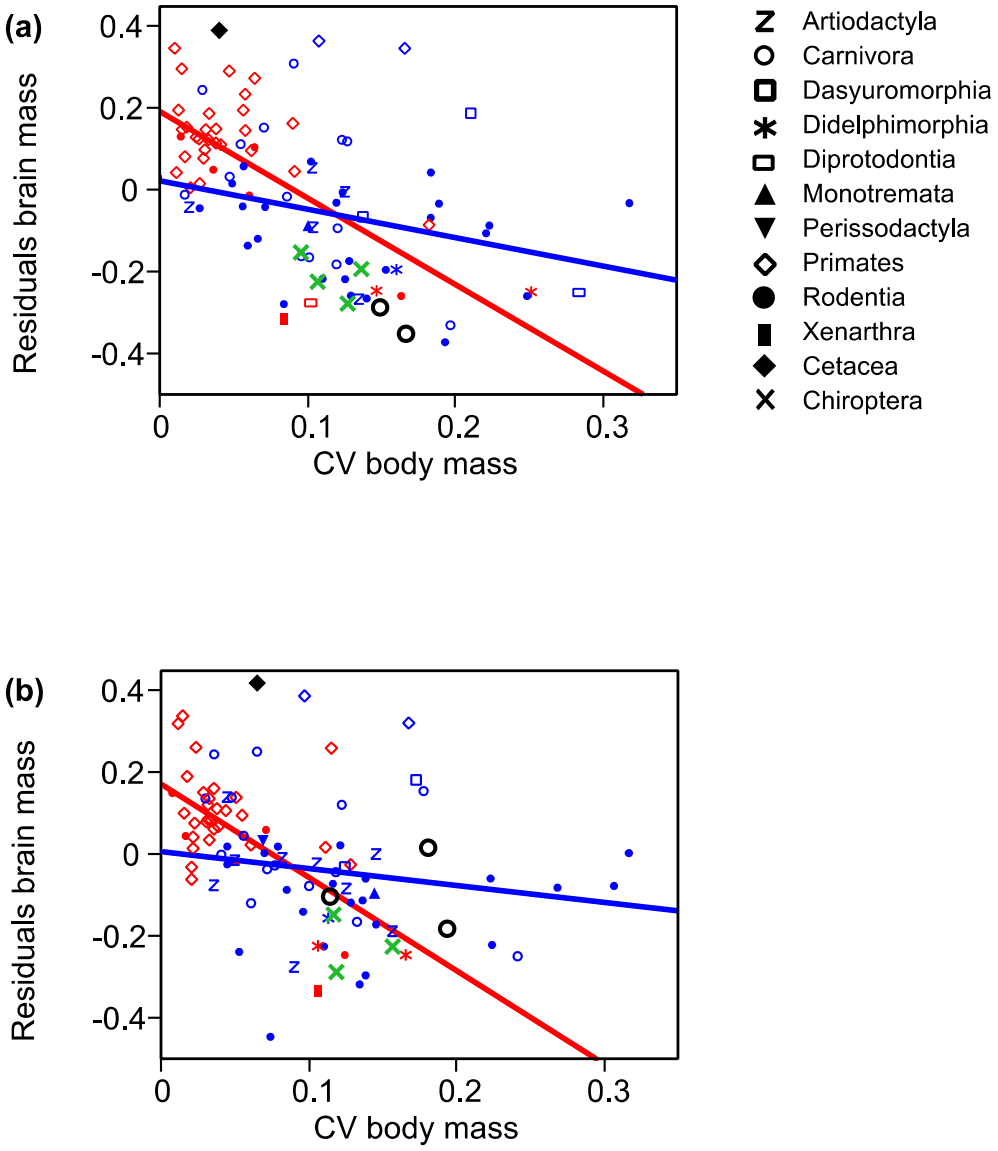


Figure S4. Relationship between log(brain size) and CV body mass in males (**a**) and in females (**b**), for the two types of substrate use (raw species values, blue = terrestrial, red = arboreal). Aquatic = black and volant species = green are not included in the calculation of the correlation and are only shown for illustrative purposes.

Supplementary context and discussion

Energetic costs of locomotion associated with larger adipose depots

This section contains a discussion of the current state of the literature about locomotor costs associated with transporting body fat.

Evidence that increased locomotor costs are directly associated with larger adipose deposits mostly derives from studies in humans. Generally, body fat percentage was positively related to total energy expenditure in a large sample of humans living in five different populations (Pontzer et al., 2016b). Obese subjects expended more metabolic energy (per kg body weight or matched for body mass) during walking compared to leaner subjects (Volpe and Bar-Or, 2003; Browning et al., 2006). Other studies found that within subjects, a reduction in body fat mass reduced the energy costs of walking and running (Foster et al., 1995; Ghiani et al., 2015). Furthermore, in both women and men body fat content is inversely related to both sprint performance (Thorland et al., 1987; Deason et al., 1991; Meckel et al., 1995) and endurance running or long-distance inline skating performance (Sparling and Cureton, 1983; Knechtle et al., 2011).

In horses, race time was positively correlated to fat mass and percentage body fat (Kearns et al., 2002) and top finishers in a 150-mile endurance race had approximately 20 kg less body fat than horses that abandoned the race (Lawrence et al., 1992). In fat-tailed dwarf lemurs (*Cheirogaleus medius*), the individual with the heavier tail comprising a higher amount of body fat storage ran at significantly lower speed than did the individual with the lighter tail (Young et al., 2007). Russian ground squirrels (*Citellus* spp.) that lay down large quantities of adipose tissue became very sluggish when fat (Owen, 1868). And lastly, in king penguins (*Aptenodytes patagonicus*), heavy ones returning from the sea were more likely to fall over than the lighter ones that had been fasting (Willener et al., 2016). This was attributed to a less stable upright posture due to the more anterior position of the centre of mass, as fat is accumulated mainly ventrally.

The metabolic cost of carrying fat during locomotion in humans is similar to the cost of carrying external loads (Griffin et al., 2003; Browning et al., 2006). For load carriage, several animal studies demonstrated effects on locomotor parameters such as a reduction in speed, an increased duty factor, an elevated metabolic rate, and a higher heart rate (Taylor et al., 1980; Oldruitenborgh-Oosterbaan et al., 1995; Baudinette and Biewener, 1998; Wickler et al., 2001; Lee et al., 2004; Young et al., 2007). Based on these findings we conclude that it is justified to assume that an increased percentage of adipose depots significantly increases locomotor costs.

Effects of substrate use on the relationship between brain size and CV body mass

This section contains additional aspects of the effect of substrate use on the relationship between brain size and CV body mass.

The expensive brain framework postulates that one way of paying the costs of an evolutionary increase in brain size is by reducing allocation to other expensive functions, such as locomotion (Isler and van Schaik, 2009). Several studies provide preliminary support for this idea. First, among terrestrial mammals brain size is negatively correlated with maximum metabolic rate, a proxy for exercise frequency and capacity (Raichlen and Gordon, 2011). Second, migratory bat species have smaller brains than sedentary ones, indicating a trade-off between brain size and locomotion costs (McGuire and Ratcliffe, 2011). Third, there is a negative correlation between brain size and pectoral muscle mass in birds (Isler and van Schaik, 2006), suggesting a role for the relative cost of flight.

Based on the findings flowing from the expensive brain framework, we predicted that the relationship between brain size and the potential to store fat (as proxied by CV body mass) is influenced by substrate use and the locomotion costs associated with it. Consistent with the existence of an allocation trade-off between locomotion costs and brain size, we did indeed find a stronger trade-off between brain size and body fat (CV body mass) in arboreal clades compared to terrestrial ones. Furthermore, in our dataset, arboreal species exhibited less seasonal variation in body mass than terrestrial mammals, suggesting that they are less prone to store fat. However, our sample of arboreal mammals is heavily biased towards primates, as body mass data of more arboreal non-primate mammals are presently lacking. But in agreement with our findings, a study in *Macaca sinica*, a largely arboreal macaque species, also found a very low percentage of total body fat (about 2% of body weight) (Dittus, 2013). For future studies it would be interesting to compare the amount of body fat of arboreal versus terrestrial primates, which was not possible in this study due to the small number of predominantly terrestrial primate species (*Pan troglodytes* and *Macaca fuscata*) available in our study.

Arboreal versus terrestrial substrate use

We found a stronger trade-off between brain size and CV body mass in arboreal compared to terrestrial clades. One reason for this finding could be that climbing involves much higher costs of transporting additional weight than moving horizontally. For instance, Hanna and colleagues (2008) have shown that for most primate species vertical climbing entails higher energetic cost than speed-matched level walking. Furthermore, the authors found that these costs of climbing were particularly high for larger primates (more than 0.5 kilograms). A comparative study on prosimians (Warren and Crompton, 1998) found that the species with highest energetic costs in upwards- and downwards-directed locomotion, the greater galago (*Otolemur crassicaudatus*), also exhibited the highest body mass of their sample.

Leaping and vertical clinging are common locomotor behaviours of several arboreal species (e.g., Fleagle and Mittermeier, 1980; Crompton, 1984; Warren and Crompton, 1998; Essner, 2002; Youlatos and Samaras, 2011). These behaviours are also likely to be affected by body fat, as additional adipose depots reduce the proportion of muscle mass relative to total body mass, and thus increase the muscle work needed to increase the potential energy of the centre of mass during the take-off part of a leap. Studies of domestic cats (Harris and Steudel, 2002) and humans (McLeod et al., 1983; Davis et al., 2003) showed that body fat was a strong predictor of the maximum vertical jumping performance in both species. Schradin and Anzenberger (2001) measured the distance individual common marmosets were able to leap without carrying infants and when carrying infants of different weights. They found a significant negative correlation between infant load and maximum leaping distance. This finding suggests that an additional load in the form of body fat might also impede the leaping distance and hence negatively affect foraging efficiency and, especially, predator avoidance, leading to a stronger brain-fat trade-off in arboreal compared to terrestrial clades.

Volant and aquatic species

Flying mammals such as bats are expected to have even higher costs of transporting adipose depots compared to terrestrial and arboreal clades. In our sample, the three species of bats for which CV body mass data were available exhibit a relatively high CV body mass and small brains, even compared to arboreal mammals. However, the small number of species does not allow any conclusions about a potential trade-off in this clade. The costs of carrying body fat are expected to be particularly high among those bat species whose predominant mode of locomotion is flapping flight, the most energetically expensive mode of locomotion (Chai and Dudley, 1995; Norberg, 2012).

A comparative study of body composition in bats has not been conducted yet, to our knowledge. But one study in birds noted that artificially loaded house sparrows had a reduced ability to take-off, implying that additional load in the form of body fat might also impede flight abilities (Blem, 1975).

The highest levels of fatness are expected in semi-aquatic or aquatic species, where large size and volume do not increase cost of transport due to buoyancy, as long as geometric similarity of the body form is maintained (Marino, 1998; Pond, 1998; Alexander, 2003). Interestingly, northern elephant seals (*Mirounga angustirostris*) increased their fat stores during migration, became neutrally buoyant divers and gained energetic advantages via reduced swimming costs (Adachi et al., 2014). This reduction in swimming cost suggests a potential foraging benefit of increased adipose depots as fatter northern elephant seals spent more time foraging at greater depths allowing them to increase the energy gained during foraging, as they forage primarily at the bottom of their dives (Naito et al., 2013). Similar foraging benefits were also proposed in southern elephant seals (*Mirounga leonina*) (Thums et al., 2013; Richard et al., 2014) and grey seals (*Halichoerus grypus*) (Beck et al., 2003) where fatter individuals show longer dive durations than leaner ones.

In sum, fat storage does not seem to hamper but rather to enhance locomotor efficiency in aquatic species. It seems likely, therefore, that an aquatic lifestyle not only allows a higher total amount of body fat compared to terrestrial and arboreal species but also does not entail a brain-fat trade-off, allowing the combination of both strategies, fat storage and brain enlargement, to buffer seasonally lean periods,. In agreement with this, several marine or semi-aquatic mammals, such as whales and dolphins, seals, sea lions and beavers, exhibit both a relatively large brain and large adipose depots compared to other mammals (Marino, 1998; Pond, 1998). However, the few data points available for aquatic species in our study (three pinniped species and the bottle-nose dolphin *Tursiops truncatus*) do not allow us to test for the presence of a brain-fat trade-off in aquatic mammals. Moreover, in aquatic mammals, CV body mass may not be a good proxy for the tendency to store body fat, as fat stores are never really depleted but stay relatively high throughout the year, at least in healthy individuals.

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Datasets

Male dataset

Genus species	CV body mass	body mass [g]	Ref. CV body mass and body mass	brain size [cc]	*n* brains	Ref. brain size	number of months	provenience	lifestyle
Alces alces	0.133	454600.00	Franzmann et al 1977	483.33	6	Graber and Heldstab unpubl. data	10	1	0
Capreolus capreolus	0.102	22233.00	Gehr, personal communication	107.50	6	Graber and Heldstab unpubl. data	5	1	0
Odocoileus hemionus	0.124	59724.00	Jacobsen 2008	194.67	6	Graber and Heldstab unpubl. data	11	0	0
Redunca fulvorufula	0.019	30225.00	Skinner 1980	106.00	7	Graber and Heldstab unpubl. data	4	1	0
Rupicapra rupicapra	0.103	40000.00	Schaschl et al 2012	117.83	2	Warncke 1908	11	1	0
Canis latrans	0.122	14250.00	Poulle et al 1995	89.10	6	Graber and Heldstab unpubl. data	4	1	0
Canis lupus	0.016	33122.92	Seal and Mech 1983	123.60	8	Graber and Heldstab unpubl. data	12	0	0
Halichoerus grypus	0.155	242000.00	Beck et al 2003	300.00	1	Graber and Heldstab unpubl. data	5	1	NA
Lycaon pictus	0.054	23799.00	Visee 2001	128.33	6	Graber and Heldstab unpubl. data	4	0	0
Meles meles	0.119	10275.00	Page et al 1994	42.43	7	Graber and Heldstab unpubl. data	12	1	0
Mephitis mephitis	0.195	3030.30	Verts 1967	10.05	10	Graber and Heldstab unpubl. data	11	1	0
Mustela putorius	0.118	1110.00	Korhonen and Harri 1986	6.71	3	Graber and Heldstab unpubl. data	12	0	0
Neovison_vison	0.094	1130.76	Dunstone 1993	7.00	7	Graber and Heldstab unpubl. data	12	1	0
Pagophilus groenlandicus	0.139	141000.00	Ochoa-Acuña et al 2009	230.33	6	Graber and Heldstab unpubl. data	4	0	NA
Procyon lotor	0.126	5156.25	Moore and Kennedy 1985	41.90	10	Graber and Heldstab unpubl. data	12	1	0
Spilogale_putorius	0.100	700.47	Crabb 1944	5.00	around 20	Gittleman 1986	12	1	0
Urocyon cinereoargenteus	0.069	3723.00	Sullivan 1956	35.80	10	Graber and Heldstab unpubl. data	4	1	0
Viverra tangalunga	0.085	3701.50	Colon 2002	24.05	NA	Gittleman 1986	8	1	0
Vulpes lagopus	0.089	2748.00	Prestrud and Nilssen 1992	41.00	12	Graber and Heldstab unpubl. data	4	1	0
Vulpes rueppellii	0.028	1688.64	Olferman 1996	24.43	7	Graber and Heldstab unpubl. data	11	1	0
Vulpes vulpes	0.046	6942.42	Fairley 1970	42.30	12	Graber and Heldstab unpubl. data	11	1	0
Tursiops truncatus	0.037	260500.00	Delfinarium Duisburg	1386.67	6	Graber and Heldstab unpubl. data	12	0	NA
Eptesicus fuscus	0.118	14.90	Beer and Richards 1956	0.24	1	Baron et al 1996	12	1	NA

Genus species	CV body mass	body mass [g]	Ref. CV body mass and body mass	brain size [cc]	n brains	Ref. brain size	number of months	provenience	lifestyle
Molossus_molossus	0.089	15.50	Barros et al 2013	0.32	24	Baron et al 1996	4	1	NA
Myotis lucifugus	0.099	8.17	Kunz et al 1998	0.17	8	Baron et al 1996	4	1	NA
Scotophilus heathii	0.127	94.69	Srivastava and Krishna 2008	1.14	10	Baron et al 1996	12	1	NA
Tadarida brasiliensis	0.039	11.42	Pagels 1975	NA	NA	NA	12	1	NA
Antechinus stuartii	0.209	18.58	Banks and Dickman 2000	0.76	NA	Ashwell 2008	4	1	0
Sminthopsis crassicaudata	0.136	14.98	Morton 1978	0.36	NA	NA	12	1	0
Caluromys philander	0.145	338.00	Julien-Laferrière, personal communication	2.40	2	Graber and Heldstab unpubl. data	12	1	1
Didelphis marsupialis	0.250	1161.00	Julien-Laferrière, personal communication	5.92	6	Graber and Heldstab unpubl. data	12	1	1
Philander opossum	0.159	541.00	Julien-Laferrière, personal communication	3.83	NA	NA	12	1	0
Lasiorhinus latifrons	0.282	23702.50	Taggart et al 2005	55.50	NA	Ashwell 2008	12	1	0
Trichosurus vulpecula	0.101	2907.24	Bamford 1970	10.96	6	Graber and Heldstab unpubl. data	4	1	1
Elephantulus edwardii	0.025	50.68	Fleming and Nicolson 2002, 2003	NA	NA	NA	9	1	0
Tachyglossus aculeatus	0.099	4100.00	Nicol and Andersen 2007	22.08	6	Graber and Heldstab unpubl. data	12	1	0
Callithrix jacchus	0.057	406.45	Primate station University of Zurich, personal communication	8.25	6	Isler and van Woerden compilation	12	0	1
Cheirogaleus medius	0.181	217.00	Mueller 1999	2.53	10	Isler and van Woerden compilation	9	0	1
Daubentonia madagascariensis	0.009	2678.54	Zehr et al 2014	43.89	3	Isler et al 2008	12	0	1
Eulemur albifrons	0.089	1995.71	Zehr et al 2014	22.89	16	Isler and van Woerden compilation	12	0	1
Eulemur collaris	0.029	2281.71	Zehr et al 2014	21.99	16	Isler and van Woerden compilation	12	0	1
Eulemur coronatus	0.037	1611.65	Zehr et al 2014	19.04	9	Isler and van Woerden compilation	12	0	1
Eulemur fulvus	0.061	2664.76	Zehr et al 2014	24.69	8	Isler and van Woerden compilation	12	0	1
Eulemur macaco	0.040	2339.43	Zehr et al 2014	22.89	11	Isler and van Woerden compilation	12	0	1
Eulemur mongoz	0.023	1495.24	Zehr et al 2014	16.86	8	Isler and van Woerden compilation	12	0	1
Eulemur rubriventer	0.014	2080.18	Zehr et al 2014	23.13	11	Isler and van Woerden compilation	12	0	1

Genus species	CV body mass	body mass [g]	Ref. CV body mass and body mass	brain size [cc]	*n* brains	Ref. brain size	number of months	provenience	lifestyle
Eulemur rufus	0.032	2180.53	Zehr et al 2014	22.42	19	Isler and van Woerden compilation	12	0	1
Eulemur sanfordi	0.057	2035.95	Zehr et al 2014	22.50	1	Isler and van Woerden compilation	12	0	1
Galago moholi	0.017	181.77	Zehr et al 2014	3.76	32	Isler and van Woerden compilation	12	0	1
Hapalemur griseus	0.030	1017.16	Zehr et al 2014	13.41	16	Isler and van Woerden compilation	12	0	1
Lemur catta	0.016	2541.96	Zehr et al 2014	22.79	17	Isler and van Woerden compilation	12	0	1
Leontopithecus rosalia	0.046	620.00	Dietz et al 1994	12.99	8	Isler and van Woerden compilation	12	1	1
Loris tardigradus	0.014	184.97	Zehr et al 2014	5.34	9	Isler and van Woerden compilation	12	0	1
Macaca fuscata	0.164	9300.00	Muroyama et al 2006	110.38	5	Isler and van Woerden compilation	12	1	0
Microcebus murinus	0.090	76.53	Zehr et al 2014	1.54	23	Isler and van Woerden compilation	12	0	1
Microcebus rufus	0.063	40.14	Randrianambinina et al 2003	1.61	7	Isler and van Woerden compilation	7	1	1
Mirza coquereli	0.011	288.61	Zehr et al 2014	5.86	3	Isler and van Woerden compilation	12	0	1
Nycticebus coucang	0.020	1087.08	Zehr et al 2014	10.23	27	Isler and van Woerden compilation	12	0	1
Nycticebus pygmaeus	0.025	485.40	Zehr et al 2014	7.38	4	Isler and van Woerden compilation	12	0	1
Otolemur garnettii	0.026	1203.97	Zehr et al 2014	11.24	22	Isler and van Woerden compilation	12	0	1
Pan troglodytes	0.106	42000.00	Uehara and Nishida 1987	344.40	80	Isler and van Woerden compilation	9	1	0
Perodicticus potto	0.032	851.19	Zehr et al 2014	12.79	67	Isler and van Woerden compilation	12	0	1
Propithecus coquereli	0.010	3735.99	Zehr et al 2014	27.45	2	Isler and van Woerden compilation	12	0	1
Propithecus verreauxi	0.055	2026.00	Lewis and Kappeler 2005	25.35	10	Isler and van Woerden compilation	7	1	1
Varecia rubra	0.028	3543.10	Zehr et al 2014	28.90	4	Isler and van Woerden compilation	12	0	1
Varecia variegata	0.037	3436.82	Zehr et al 2014	30.83	8	Isler and van Woerden compilation	12	0	1
Acomys subspinosus	0.079	17.05	Fleming and Nicolson 2002, 2003	NA	NA	NA	6	1	0

Genus species	CV body mass	body mass [g]	Ref. CV body mass and body mass	brain size [cc]	*n* brains	Ref. brain size	number of months	provenience	lifestyle
Aethomys chrysophilus	0.026	76.70	Korn 1989	1.25	usually 6	Mace et al 1981	12	NA	0
Akodon azarae	0.312	19.38	Del Valle and Busch 2003	NA	NA	NA	4	1	0
Bandicota bengalensis	0.216	179.80	Kaur and Guraya 1983	NA	NA	NA	12	NA	0
Callosciurus erythraeus	0.027	354.21	Tamura and Terauchi 1994	NA	NA	NA	12	1	1
Ctenomys talarum	0.065	89.41	Del Valle et al 2006	NA	NA	NA	4	1	0
Cynomys leucurus	0.247	1139.00	Tileston and Lechtleitner 1966	5.69	usually 6	Mace et al 1981	6	1	0
Cynomys ludovicianus	0.187	776.00	Tileston and Lechtleitner 1966	7.25	usually 6	Mace et al 1981	9	1	0
Erethizon dorsatum	0.162	8885.71	Sweitzer and Berger 1993	26.33	6	Graber and Heldstab unpubl. data	7	1	1
Funambulus tristriatus	0.067	128.20	Advani and Sujatha 1984	NA	NA	NA	12	1	1
Gerbilliscus brantsii	0.048	83.58	Korn 1989	1.56	usually 6	Mace et al 1981	12	NA	0
Gerbilliscus leucogaster	0.065	72.92	Korn 1989	NA	NA	NA	12	NA	0
Marmota flaviventris	0.192	3900.00	Zatzman et al 1984	10.96	6	Graber and Heldstab unpubl. data	6	1	0
Marmota marmota	0.109	4050.00	Koertner and Heldmaier 1995	16.10	3	Pilleri 1959	12	0	0
Marmota monax	0.124	3100.00	Concannon et al 2001	13.13	2	Graber and Heldstab unpubl. data	12	0	0
Mastomys natalensis	0.152	63.50	Korn 1989	0.77	usually 6	Mace et al 1981	12	NA	0
Meriones unguiculatus	0.122	57.70	Zhang and Wang 2007	1.13	usually 6	Mace et al 1981	4	1	0
Micaelamys namaquensis	0.083	47.20	Korn 1989	0.52	NA	Bernard and Nurton 1993	12	NA	0
Microtus cabrerae	0.058	52.70	Fernandez-Salvador 2004	NA	NA	NA	12	1	0
Microtus californicus	0.058	51.90	Batzli and Pitelka 1971	0.78	usually 6	Mace et al 1981	12	1	0
Microtus ochrogaster	0.222	39.58	Voltura 1997	0.71	usually 6	Mace et al 1981	4	1	0
Microtus pennsylvanicus	0.316	38.20	Iverson and Turner 1974	0.77	usually 6	Mace et al 1981	12	1	0
Myodes rutilus	0.182	19.28	Zuercher et al 1999	0.56	usually 6	Mace et al 1981	4	1	0
Oryzomys palustris	0.070	45.86	Cameron and Spencer 1983	0.88	usually 6	Mace et al 1981	12	1	0
Peromyscus leucopus	0.055	20.50	Lynch 1973	0.60	123	Mace and Eisenberg 1982	5	1	0
Rattus fuscipes	0.118	102.25	Banks and Dickman 2000	1.63	usually 6	Mace et al 1981	4	1	0
Rattus villosissimus	0.164	158.50	Carstairs 1980	NA	NA	NA	5	1	0
Reithrodontomys fulvescens	0.065	11.48	Cameron and Spencer 1983	NA	NA	NA	12	1	0
Rhabdomys pumilio	0.065	42.20	Korn 1989	0.69	usually 6	Mace et al 1981	12	NA	0

Genus species	CV body mass	body mass [g]	Ref. CV body mass and body mass	brain size [cc]	*n* brains	Ref. brain size	number of months	provenience	lifestyle
Saccostomus mearnsi	0.091	79.50	Keesing 1998	NA	NA	NA	5	1	0
Sciurus carolinensis	0.063	450.42	Short and Duke 1971	6.63	6	Graber and Heldstab unpubl. data	12	0	1
Sciurus nayaritensis	0.029	677.50	Pasch and Koprowski 2006	NA	NA	NA	4	1	1
Sciurus niger	0.059	775.00	Short and Duke 1971	7.50	6	Graber and Heldstab unpubl. data	12	0	1
Sciurus vulgaris	0.013	299.50	Lurz and Lloyd 2000	5.25	6	Graber and Heldstab unpubl. data	12	1	1
Sigmodon hispidus	0.127	98.89	Cameron and Spencer 1983	1.14	usually 6	Mace et al 1981	12	1	0
Spermophilus citellus	0.128	396.00	Millesi et al 1999	2.66	5	Graber and Heldstab unpubl. data	7	1	0
Spermophilus franklinii	0.219	410.00	Choromanski-Norris et al 1986	3.82	usually 6	Mace et al 1981	5	1	0
Spermophilus lateralis	0.182	235.70	Blake 1972	2.75	11	Graber and Heldstab unpubl. data	12	0	0
Spermophilus parryii	0.139	902.33	Buck and Barnes 1999	4.83	6	Graber and Heldstab unpubl. data	6	1	0
Spermophilus saturatus	0.026	259.00	Kenagy et al 1989	NA	NA	NA	12	1	0
Tamias striatus	0.101	113.00	Levesque and Tattersall 2010	2.17	usually 6	Mace et al 1981	12	0	0
Tamiasciurus hudsonicus	0.035	237.90	Koprowski 2005	3.67	6	Graber and Heldstab unpubl. data	12	1	1
Zapus hudsonius	0.055	17.50	Morrison and Ryser 1962	0.43	usually 6	Mace et al 1981	12	0	0
Bradypus variegatus	0.083	4888.25	Silva et al 2014	14.89	13	Crile and Quiring 1940	12	1	1

Female dataset

Genus species	CV body mass	body mass [g]	Ref. CV body mass and body mass	brain size [cc]	*n* brains	Ref. brain size	lifestyle	number of months	provenience	reproductive status
Alces alces	0.090	400500.00	Franzmann et al 1977	483.33	6	Graber and Heldstab unpubl. data	0	12	1	0
Capreolus capreolus	0.082	23808.00	Gehr, personal communication	107.50	6	Graber and Heldstab unpubl. data	0	5	1	0
Dama dama	0.045	34150.00	Weber and Thompson 1998	195.83	6	Graber and Heldstab unpubl. data	0	12	0	1
Odocoileus hemionus	0.050	54073.00	Jacobsen 2008	194.67	6	Graber and Heldstab unpubl. data	0	11	0	0
Ovibos moschatus	0.125	144000.00	Adamczewski et al 1997	350.00	7	Graber and Heldstab unpubl. data	0	7	1	0
Potamochoerus porcus	0.156	64120.00	Tierpark Hellabrunn, München, personal communication	150.19	10	Bauchot 1985	0	5	0	0
Rangifer tarandus	0.145	92330.00	Chan-McLeod et al 1999	305.36	14	Graber and Heldstab unpubl. data	0	4	1	0
Redunca fulvorufula	0.036	28600.00	Skinner 1980	106.00	7	Graber and Heldstab unpubl. data	0	4	1	0
Rupicapra rupicapra	0.105	27166.67	Schaschl et al 2012	113.74	2	Warncke 1908	0	11	1	0
Canis latrans	0.122	12500.00	Poulle et al 1995	89.10	6	Graber and Heldstab unpubl. data	0	4	1	0
Canis lupus	0.041	28001.39	Seal and Mech 1983	123.60	8	Graber and Heldstab unpubl. data	0	12	0	0
Halichoerus grypus	0.179	159400.00	Beck et al 2003	300.00	1	Graber and Heldstab unpubl. data	NA	5	1	0
Lycaon pictus	0.030	19568.00	Visee 2001	128.33	6	Graber and Heldstab unpubl. data	0	4	0	0
Meles meles	0.132	11220.83	Page et al 1994	42.43	7	Graber and Heldstab unpubl. data	0	12	1	0
Mephtitis mephitis	0.240	2150.54	Verts 1967	10.05	10	Graber and Heldstab unpubl. data	0	11	1	0
Mustela putorius	0.061	689.00	Korhonen and Harri 1986	5.79	6	Graber and Heldstab unpubl. data	0	12	0	0
Neovison vison	0.072	691.85	Dunstone 1993	7.00	7	Graber and Heldstab unpubl. data	0	9	1	0
Otaria flavescens	0.105	120690.43	Tierpark Hellabrunn, München, personal communication	288.33	6	Graber and Heldstab unpubl. data	NA	6	0	0
Procyon lotor	0.177	4188.89	Moore and Kennedy 1985	41.90	10	Graber and Heldstab unpubl. data	0	9	1	0
Spilogale putorius	0.100	501.78	Crabb 1944	5.00	around 20	Gittleman 1986	0	10	1	0
Urocyon cinereoargenteus	0.048	3541.00	Sullivan 1956	35.80	10	Graber and Heldstab unpubl. data	0	4	1	0
Ursus thibetanus	0.118	87500.00	Hashimoto and Yasutake 1999	261.88	8	Graber and Heldstab unpubl. data	0	8	0	0
Viverra tangalunga	0.077	3485.40	Colon 2002	24.05	NA	Gittleman 1986	0	8	1	1
Vulpes lagopus	0.065	3019.00	Prestrud and Nilssen 1992	41.00	12	Graber and Heldstab unpubl. data	0	4	1	0
Vulpes rueppellii	0.036	1532.95	Olferman 1996	24.43	7	Graber and Heldstab unpubl. data	0	11	1	0

Genus species	CV body mass	body mass [g]	Ref. CV body mass and body mass	brain size [cc]	*n* brains	Ref. brain size	lifestyle	number of months	provenience	reproductive status
Vulpes vulpes	0.056	5620.00	Fairley 1970	40.86	14	Graber and Heldstab unpubl. data	0	10	1	0
Zalophus californianus	0.167	86792.00	Tierpark Hellabrunn, München, personal communication	292.86	7	Graber and Heldstab unpubl. data	NA	5	0	0
Tursiops truncatus	0.059	211185.19	Delfinarium Duisburg, homepage	1386.67	6	Graber and Heldstab unpubl. data	NA	11	0	1
Eptesicus fuscus	0.109	18.67	Beer and Richards 1956	0.23	1	Baron et al 1996	NA	12	1	1
Myotis lucifugus	0.108	8.16	Kunz et al 1998	0.16	8	Baron et al 1996	NA	4	1	0
Scotophilus heathii	0.150	35.75	Srivastava and Krishna 2008	0.46	10	Baron et al 1996	NA	12	1	0
Tadarida brasiliensis	0.100	12.88	Pagels 1975	NA	NA	NA	NA	12	1	0
Antechinus stuartii	0.172	18.58	Banks and Dickman 2000	0.76	NA	Ashwell 2008	0	4	1	0
Sminthopsis crassicaudata	0.124	13.22	Morton 1978	0.36	NA	Ashwell 2008	0	12	0	0
Caluromys philander	0.106	292.00	Julien-Laferrière, personal communication	2.40	2	Graber and Heldstab unpubl. data	1	12	1	0
Didelphis marsupialis	0.165	1040.00	Julien-Laferrière, personal communication	5.92	6	Graber and Heldstab unpubl. data	1	12	1	0
Philander opossum	0.113	444.00	Julien-Laferrière, personal communication	3.83	NA	Ashwell 2008	0	11	1	0
Elephantulus edwardii	0.126	50.68	Fleming and Nicolson 2002, 2003	NA	NA	NA	0	11	1	0
Tachyglossus aculeatus	0.144	3800.00	Nicol and Andersen 2007	22.08	6	Graber and Heldstab unpubl. data	0	11	1	0
Equus caballus	0.069	250000.00	Scheibe and Streich 2003	693.00	NA	Kruska 1973	0	6	0	0
Callithrix jacchus	0.018	409.36	Primate station Univeristy of Zurich, personal communication	7.90	17	Isler and van Woerden compilation	1	12	0	1
Cheirogaleus medius	0.128	172.00	Mueller 1999	2.54	19	Isler and van Woerden compilation	1	7	0	1
Daubentonia madagascariensis	0.012	2650.87	Zehr et al 2014	43.20	10	Isler et al 2008	1	12	0	1
Eulemur albifrons	0.055	2310.34	Zehr et al 2014	23.31	7	Isler and van Woerden compilation	1	12	0	1
Eulemur collaris	0.023	2454.96	Zehr et al 2014	23.50	13	Isler and van Woerden compilation	1	12	0	1
Eulemur coronatus	0.029	1581.55	Zehr et al 2014	20.08	5	Isler and van Woerden compilation	1	12	0	1
Eulemur fulvus	0.044	2391.91	Zehr et al 2014	24.78	8	Isler and van Woerden compilation	1	12	0	1
Eulemur macaco	0.031	2501.04	Zehr et al 2014	24.07	8	Isler and van Woerden compilation	1	12	0	1
Eulemur mongoz	0.032	1614.95	Zehr et al 2014	19.08	11	Isler and van Woerden compilation	1	12	0	1
Eulemur rubriventer	0.038	2339.52	Zehr et al 2014	24.62	13	Isler and van Woerden compilation	1	12	0	1
Eulemur rufus	0.034	2247.23	Zehr et al 2014	22.31	11	Isler and van Woerden compilation	1	12	0	1

Genus species	CV body mass	body mass [g]	Ref. CV body mass and body mass	brain size [cc]	*n* brains	Ref. brain size	lifestyle	number of months	provenience	reproductive status
Eulemur sanfordi	0.032	2094.17	Zehr et al 2014	21.25	2	Isler and van Woerden compilation	1	12	0	1
Galago moholi	0.036	157.63	Zehr et al 2014	3.63	33	Isler and van Woerden compilation	1	12	0	1
Hapalemur griseus	0.033	1024.71	Zehr et al 2014	13.97	21	Isler and van Woerden compilation	1	12	0	1
Lemur catta	0.022	2401.02	Zehr et al 2014	21.37	7	Isler and van Woerden compilation	1	12	0	1
Leontopithecus rosalia	0.024	598.00	Dietz et al 1994	12.48	10	Isler and van Woerden compilation	1	12	1	0
Loris tardigradus	0.015	173.36	Zehr et al 2014	5.84	4	Isler and van Woerden compilation	1	12	0	1
Macaca fuscata	0.167	7750.00	Muroyama et al 2006	97.90	6	Isler and van Woerden compilation	0	12	1	0
Microcebus murinus	0.111	84.27	Zehr et al 2014	1.64	21	Isler and van Woerden compilation	1	12	0	1
Microcebus rufus	0.115	43.80	Randrianambinina et al 2003	1.72	10	Isler and van Woerden compilation	1	7	1	0
Mirza coquereli	0.016	312.89	Zehr et al 2014	5.32	3	Isler and van Woerden compilation	1	12	0	1
Nycticebus coucang	0.021	1195.64	Zehr et al 2014	10.03	28	Isler and van Woerden compilation	1	12	0	1
Nycticebus pygmaeus	0.033	495.95	Zehr et al 2014	6.47	1	Isler and van Woerden compilation	1	12	0	1
Otolemur garnettii	0.022	977.53	Zehr et al 2014	10.20	13	Isler and van Woerden compilation	1	12	0	1
Pan troglodytes	0.097	35200.00	Uehara and Nishida 1987	357.71	79	Isler and van Woerden compilation	0	9	1	0
Perodicticus potto	0.051	823.56	Zehr et al 2014	12.02	44	Isler and van Woerden compilation	1	12	0	1
Propithecus coquereli	0.021	4154.01	Zehr et al 2014	27.37	3	Isler and van Woerden compilation	1	12	0	1
Propithecus verreauxi	0.061	3201.50	Lewis and Kappeler 2005	25.60	13	Isler and van Woerden compilation	1	7	1	0
Varecia rubra	0.039	3557.13	Zehr et al 2014	30.43	6	Isler and van Woerden compilation	1	12	0	1
Varecia variegata	0.036	3527.23	Zehr et al 2014	30.01	14	Isler and van Woerden compilation	1	12	0	1
Acomys subspinosus	0.168	17.05	Fleming and Nicolson 2002, 2003	NA	NA	NA	0	7	1	0
Aethomys chrysophilus	0.045	68.10	Korn 1989	1.25	usually 6	Mace et al 1981	0	12	NA	0
Akodon azarae	0.309	15.51	Del Valle and Busch 2003	NA	NA	NA	0	4	1	0
Bandicota bengalensis	0.253	179.80	Kaur and Guraya 1983	NA	NA	NA	0	12	NA	0
Callosciurus erythraeus	0.065	355.42	Tamura and Terauchi 1994	NA	NA	NA	1	11	1	0
Ctenomys talarum	0.065	31.26	Del Valle et al 2006	NA	NA	NA	0	4	1	0
Cynomys leucurus	0.110	925.00	Tileston and Lechtleitner 1966	5.69	usually 6	Mace et al 1981	0	6	1	0
Cynomys ludovicianus	0.222	776.00	Tileston and Lechtleitner 1966	7.25	usually 6	Mace et al 1981	0	11	1	0
Erethizon dorsatum	0.124	7114.29	Sweitzer and Berger 1993	24.92	6	Graber and Heldstab unpubl. data	1	7	1	0

Genus species	CV body mass	body mass [g]	Ref. CV body mass and body mass	brain size [cc]	*n* brains	Ref. brain size	lifestyle	number of months	provenience	reproductive status
Funambulus tristriatus	0.069	123.10	Advani and Sujatha 1984	NA	NA	NA	1	12	1	0
Gerbilliscus brantsii	0.045	79.85	Korn 1989	1.56	usually 6	Mace et al 1981	0	12	NA	0
Gerbilliscus leucogaster	0.058	69.33	Korn 1989	NA	NA	NA	0	12	NA	0
Marmota flaviventris	0.074	4356.67	Zatzman et al 1984	10.96	6	Graber and Heldstab unpubl. data	0	6	0	0
Marmota monax	0.134	3485.00	Concannon et al 2001	12.36	7	Graber and Heldstab unpubl. data	0	12	0	0
Meriones unguiculatus	0.121	51.40	Zhang and Wang 2007	1.13	usually 6	Mace et al 1981	0	4	1	1
Micaelamys namaquensis	0.138	47.45	Korn 1989	0.52	5	Bernard and Nurton 1993	0	12	NA	0
Microtus cabrerae	0.126	51.40	Fernandez-Salvador 2004	NA	NA	NA	0	12	1	0
Microtus californicus	0.085	44.11	Batzli and Pitelka 1971	0.78	usually 6	Mace et al 1981	0	12	1	1
Microtus ochrogaster	0.136	41.54	Voltura 1997	0.71	usually 6	Mace et al 1981	0	4	1	1
Microtus pennsylvanicus	0.305	41.54	Iverson and Turner 1974	0.77	usually 6	Mace et al 1981	0	12	1	0
Microtus pinetorum	0.070	21.30	Lochmiller et al 1983	0.56	usually 6	Mace et al 1981	0	6	1	0
Myodes rutilus	0.315	21.24	Zuercher et al 1999	0.56	usually 6	Mace et al 1981	0	4	1	0
Oryzomys palustris	0.079	37.08	Cameron and Spencer 1983	0.88	usually 6	Mace et al 1981	0	12	1	0
Rattus villosissimus	0.130	158.50	Carstairs 1980	NA	NA	NA	0	5	1	0
Reithrodontomys fulvescens	0.074	11.24	Cameron and Spencer 1983	NA	NA	NA	0	12	1	0
Rhabdomys pumilio	0.096	43.95	Korn 1989	0.69	usually 6	Mace et al 1981	0	12	NA	0
Saccostomus mearnsi	0.071	62.30	Keesing 1998	NA	NA	NA	0	5	1	0
Sciurus carolinensis	0.071	433.13	Short and Duke 1971	6.17	6	Graber and Heldstab unpubl. data	1	12	0	1
Sciurus nayaritensis	0.056	713.80	Pasch and Koprowski 2006	NA	NA	NA	1	4	1	0
Sciurus niger	0.051	742.08	Short and Duke 1971	7.69	6	Graber and Heldstab unpubl. data	1	12	0	1
Sciurus vulgaris	0.008	303.00	Lurz and Lloyd 2000	5.75	6	Graber and Heldstab unpubl. data	1	4	1	1
Sigmodon hispidus	0.128	80.02	Cameron and Spencer 1983	1.14	usually 6	Mace et al 1981	0	12	1	0
Spermophilus citellus	0.145	290.00	Millesi et al 1999	2.66	5	Graber and Heldstab unpubl. data	0	6	1	0
Spermophilus franklinii	0.267	351.00	Choromanski-Norris et al 1986	3.82	usually 6	Mace et al 1981	0	4	1	0
Spermophilus lateralis	0.116	211.50	Blake 1972	2.67	6	Graber and Heldstab unpubl. data	0	12	0	0
Spermophilus parryii	0.223	803.50	Buck and Barnes 1999	5.08	6	Graber and Heldstab unpubl. data	0	6	1	0
Spermophilus richardsonii	0.053	357.50	Michener 1978	2.67	6	Graber and Heldstab unpubl. data	0	6	1	0

Genus species	CV body mass	body mass [g]	Ref. CV body mass and body mass	brain size [cc]	*n* brains	Ref. brain size	lifestyle	number of months	provenience	reproductive status
Spermophilus saturatus	0.077	224.00	Kenagy et al 1989	NA	NA	NA	0	12	1	0
Tamiasciurus hudsonicus	0.017	229.50	Koprowski 2005	3.67	6	Graber and Heldstab unpubl. data	1	12	1	0
Zapus hudsonius	0.138	18.15	Morrison and Ryser 1962	0.43	usually 6	Mace et al 1981	0	4	0	0
Bradypus variegatus	0.106	4669.64	Silva et al 2014	14.89	13	Crile and Quiring 1940	1	11	1	0

Chapter 4

Getting fat or getting help?

How female mammals cope with energetic constraints on reproduction

Sandra A. Heldstab, Carel P. van Schaik, and Karin Isler

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Abstract

Background: Fat deposits enable a female mammal to bear the energy costs of offspring production and thus greatly influence her reproductive success. However, increasing locomotor costs and reduced agility counterbalance the fitness benefits of storing body fat. In species where costs of reproduction are distributed over other individuals such as fathers or non-breeding group members, reproductive females might therefore benefit from storing less energy in the form of body fat.

Results: Using a phylogenetic comparative approach on a sample of 87 mammalian species, and controlling for possible confounding variables, we found that reproductive females of species with allomaternal care exhibit reduced annual variation in body mass (estimated as CV body mass), which is a good proxy for the tendency to store body fat. Differential analyses of care behaviours such as allonursing or provisioning corroborated an energetic interpretation of this finding. The presumably most energy-intensive form of allomaternal care, provisioning of the young, had the strongest effect on CV body mass. In contrast, allonursing, which involves no additional influx of energy but distributes maternal help across different mothers, was not correlated with CV body mass.

Conclusions: Our results suggest that reproducing females in species with allomaternal care can afford to reduce reliance on fat reserves because of the helpers' energetic contribution towards offspring rearing.

Keywords: allomaternal care, cooperative breeding, body fat, paternal care, helping behaviours, reproduction, allonursing, provisioning

Background

Reproduction is energetically very expensive (McNab, 2006; Speakman, 2008) and several studies show that the amount of food available and hence the total amount of energy invested by the mother influences reproductive success in female mammals. Provisioning by humans generally leads to higher reproductive rates, shorter lactation periods, and shorter inter-birth intervals (Mori, 1979; Küster and Paul, 1984; Borries et al., 2001). In natural animal populations, higher food abundance leads to higher birth rates (Tyler, 1987; Wauters and Lens, 1995; van Noordwijk and van Schaik, 1999; Takahashi, 2002; Heesen et al., 2013; Arlet et al., 2015). In contrast, food restriction may delay sexual maturation and among adults may inhibit mating behaviour (Gill and Rissman, 1997; Cowlishaw and Dunbar, 2000; Temple et al., 2002) or even produce acyclicity or anoestrus (Wade and Schneider, 1992; Kauffman et al., 2010).

In mammals that evolved in seasonal environments and thus face periods of food scarcity, a female's ability to bear the energy costs of pregnancy and lactation, and thus her reproductive success, may be affected by the amount of body fat she can deposit. That stored body fat plays an essential role in female reproduction has been proposed previously within the capital-income-continuum concept (for a review see (Jönsson, 1997)) and empirical evidence for this idea is abundant. For instance, in rhesus macaques and moose, the size of maternal fat stores positively affects pregnancy and birth rates (Testa and Adams, 1998; Campbell and Gerald, 2004). Furthermore, numerous studies show that heavier and fatter mothers produce heavier offspring that grow faster and are more likely to survive, suggesting that females in better body condition are able to allocate more stored resources to reproduction (Schneider and Wade, 1989; Atkinson and Ramsay, 1995; Côté and Festa-Bianchet, 2001; Lewis and Kappeler, 2005; Christiansen et al., 2014; Rödel et al., 2016). Finally, several studies in seals show that body fat is essential for lactation as seal mothers lose more than 50% of their stored body fat until the end of lactation ((Bowen et al., 1992) and references therein). Significant seasonal fattening in females may also be found if they do not reproduce, e.g. to buffer environmental food fluctuations (Short and Duke, 1971; Zhang and Wang, 2007). However, because reproductive seasons and experienced seasonality in food intake are generally interrelated, it is usually impossible to disentangle these two reasons for body fat storage (Batzli and Pitelka, 1971; van Schaik and van Noordwijk, 1985; Bronson, 1989; Tyler and Blix, 1990; Réale et al., 2003). Female polar bears offer an extreme example of this. They store body fat to hibernate due to adverse environmental conditions for up to eight months while simultaneously meeting the nutritional demands of gestation and lactation during this fasting period (Atkinson and Ramsay, 1995).

But the positive effect of fat stores on fitness is counterbalanced by their costs. Large fat reserves increase the energy costs of locomotion due to higher body weight (Taylor et al., 1982; Garby et al., 1988; Ekelund et al., 2002; Peyrot et al., 2009), and also reduce agility and speed and so may compromise fitness by increasing predation risk or decreasing hunting success (Pond, 1978; Gosler et al., 1995; West and York, 1998; Dietz et al., 2007; Zamora-Camacho et al., 2014). Furthermore, in arboreal species, body fat may also impede terminal branch feeding (Dittus, 2013). Indeed, arboreal species are less prone to store fat than terrestrial ones (Heldstab et al., 2016). Therefore, we hypothesize that female mammals should minimize the amount of fat stores if they have an alternative to fuel their reproductive success.

All other things being equal, the energetic burden of reproduction on reproductive females is reduced when the costs of reproduction are distributed over several individuals. Thus, in species where other individuals provide energetic costly allomaternal care behaviours, breeding females might need to store less energy in the form of body fat themselves and could avoid the locomotion and predation costs resulting from high amounts of body fat. Allomaternal inputs are found in many mammals, comprising behaviours such as provisioning, carrying, huddling or communal nesting, babysitting, and protection from predators or defence of resources against conspecifics. The effects of such allomaternal care on offspring survival or fertility have been demonstrated within and between species (Gittleman and Oftedal, 1989; Snowdon, 1996; Mitani and Watts, 1997; Moehlman and Hofer, 1997; Ross and MacLarnon, 2000; Silk, 2007; West and Capellini, 2016). One likely mechanism underlying this effect is load-lightening of pregnant or lactating females by helpers ('load-lightening' hypothesis (Crick, 1992)) which has been demonstrated in meerkats (Scantlebury et al., 2002), callitrichids (Garber and Leigh, 1997; Bales et al., 1999) and siamangs (Lappan, 2009). This load-lightening effect has also been demonstrated in some species with facultative helping, where females can rear their pups solitarily, but under certain conditions share care for the young with one or more additional individuals. For instance, female prairie voles (*Microtus ochrogaster*) and pine voles (*Microtus pinetorum*) had shorter interlitter intervals in family groups consisting of the breeding pair and former offspring compared to families without previous offspring (Solomon, 1991; Powell and Fried, 1992). In striped mice (*Rhabdomys pumilio*) living in the succulent karoo, offspring grew faster when the father was present, which may indirectly benefit females when young are weaned earlier (Schradin and Pillay, 2005). In females of a facultatively cooperative breeding bird species, the splendid fairy-wren (*Malurus splendens*), the presence of helpers has been shown to increase survival of the breeding females and reduce the time for these females to renest after a brood (Russell and Rowley, 1988). Lastly, in another facultative cooperative breeder, the western bluebird (*Sialia mexicana*), the presence of helpers allowed the breeding female to lower her feeding rate, while nestlings still received more feeds at nests with helpers compared to nests without helpers present (Dickinson et al., 1996).

In sum, there is ample empirical evidence that distributing the costs of reproduction over two or more individuals yields an energetic benefit for mothers or offspring. We do not distinguish between the two, as a net fitness effect can be obtained by either.

Allonursing, the nursing of non-filial offspring, is another form of care that has been observed in every major mammalian lineage (Packer et al., 1992; Roulin, 2002). However, allonursing events within a species are generally rare. For instance, in tufted capuchin monkeys allosuckling accounted for 13% of all suckling events (Baldovino and Di Bitetti, 2008), in South American fur seals for around 3% (Franco-Trecu et al., 2010), and in red deer calves allosucking was even less common (Bartos et al., 2001). Furthermore, the rejection rates of suckling of non-filial offspring are high. In guanacos, for example, the rejection rate to non-filial offspring nursing attempts was three times higher than the rejection rate to filial nursing attempts (Zapata et al., 2009). Although allonursing may confer social benefits to the allonursed young (Baldovino and Di Bitetti, 2008; MacLeod et al., 2013), the energetic benefits for offspring or mother are unclear. First, allonursing is more likely to occur when several females breed concurrently (Roulin, 2002) and hence all females simultaneously bear the costs of reproduction. Therefore, the idea that allonursing functions as load-lightening mechanism for lactating females cannot apply (Clutton-Brock, 1991), and instead allonursing may serve to more evenly divide maternal energy investment across different mothers (König, 2006). Second, several studies show no apparent energetic benefits of allonursing for recipient offspring and/or mothers. For instance, red deer calves sucking only from maternal hinds increased faster in body weight than calves sucking maternal and non-maternal hinds (Bartos et al., 2001). Another study found no evidence that allonursing provides benefits to meerkat pups or mothers (MacLeod et al., 2015): pups that received allonursing were not heavier at emergence and did not have a higher survival rate than pups that did not receive allonursing. Mothers whose litters were allonursed were not in better physical condition, did not reconceive faster and did not reduce their own nursing investment compared to mothers who nursed their litters alone. To sum up, allonursing does not necessarily provide energetic benefits for the mother or offspring.

With the exception of allonursing, all other allomaternal care behaviours can be performed by all sorts of helpers in cooperatively breeding species, including fathers or non-breeding group members. Whereas the help provided by adult males (potential fathers) might be unaffected by their body condition (Clutton-Brock et al., 2002) or food abundance (Nichols et al., 2012), other non-breeding group members generally adjust their helping efforts in relation to their body condition. Furthermore, subordinates can also start to breed themselves, in which case their help to the dominant female could end abruptly or be minimal to begin with (Brouwer et al., 2011; Zöttl et al., 2013). These results suggest that paternal care is more reliable and thus more important for females than the help of others.

On the other hand, in cooperative breeders more helpers than just the father might be around to take over the energetic costs of female reproduction. The optimum amount of body fat stored by a female may therefore vary depending on whether they receive no care, paternal care or additional help from several non-breeding group members.

The aim of this study is to test whether energetic contributions towards offspring rearing through costly care allow reproductive females to reduce the amount of energy (stored as body fat) they themselves need to invest. As a proxy for the seasonal tendency to store body fat, we use data on seasonal body mass variation within a year, the coefficient of variation (CV) in body mass, which has been shown to correlate with the amount of body fat within (Heldstab et al., 2016) and across species (PGLS: $P = 0.03$, $N = 8$, $\lambda = 0$, $R^2 = 0.56$, $\beta = 0.19$, S.E. = 0.07, t = 2.74, calculated from data in (Heldstab et al., 2016)). Compared to single body fat values obtained from cadavers, CV body mass captures seasonal fluctuations, allows for a larger sample size for each species and can also be collected for wild animals (Wells, 2010). In total, both reliable information on the nature and extent of allomaternal help and sufficient data on annual variation in body mass was available for 87 species from 9 mammalian orders.

We expect that an increased energetic contribution in the form of allomaternal care provided by the male or non-breeding group members is negatively correlated with annual variation in body mass in females, because storing fat and allomaternal subsidies independently stabilize the energetic costs for female reproduction. To test this prediction, we explore the effect of different types of allomaternal help on annual body mass variation in females. On the other hand, we do not expect a correlation between allonursing behaviour and annual variation in body mass in females.

Methods

CV body mass as a proxy for the tendency to store body fat

In mammals, body fat explained between 41 and 92% of the intraspecific variation in body mass, the amount of body fat was highly correlated with carcass weight for each age and sex; hence body weight was a good predictor of total body fat (for a summary, see references in (Heldstab et al., 2016)). We therefore used seasonal changes of body mass over a year as a proxy for the tendency to store body fat. For a given species, we calculated the coefficient of variation (CV = standard deviation/mean) over monthly means of adult female body mass, yielding a total sample of 87 mammalian species from 9 orders (Additional file 1 and 2).

In a previous study we validated the use of CV body mass as a proxy for variation in body fat by showing that the monthly body mass correlated with percentage body fat in several studies that measured both in the same specimens (Heldstab et al., 2016).

We compiled monthly body mass data from the literature, including only those studies that reported monthly mean body mass for at least 4 months per year. If body mass data were given for four seasons, pooled across several months (e.g., spring, summer, autumn and winter), we set the number of months sampled to four (16 studies). In most species, monthly mean body mass data was distributed evenly across the year, except for *Antechinus stuartii*, *Lycaon pictus*, *Spermophilus franklinii* and *Zapus hudsonicus*. If several sources were available for one species, preference was given to the study with the largest sample size conducted in the wild.

Allomaternal care behaviours

In quantifying allomaternal care behaviour, we followed Isler and van Schaik (Isler and van Schaik, 2012) to obtain continuous data on the frequency of occurrence of the following care behaviours: provisioning, carrying, protection and a variable that comprises other energetically influential care behaviours such as huddling, communal nesting and pup retrieval (see Additional file 3 for a detailed description of the classification protocol). As the sample in (Isler and van Schaik, 2012) was restricted to species with known brain size, we expanded it by an additional 30 species for which data on both CV body mass and allomaternal care behaviour was available in the literature (Additional file 1 and 2). In total, CV body mass and data on allomaternal care behaviour were available for 87 species. We did not compile data for bats and cetaceans because reliable data on allomaternal care of both cetaceans and bats are notoriously difficult to obtain. Moreover, the amount of body fat and hence CV body mass as a proxy for the tendency to store body fat in these two groups may underlie different constraints than in other mammals (Marino, 1998; Pond, 1998; Alexander, 2003; Heldstab et al., 2016), precluding predictions for a combined sample.

In addition, to distinguish the effects of allomaternal care provided by males (paternal care) from that provided by other group members (care by others) we summed up the frequency of occurrence of all allomaternal care behaviours separately for the father and other group members. To investigate whether the results reported in this study are robust with respect to different coding schemes of allomaternal care, we additionally conducted all analyses by using a binary classification of all allomaternal care behaviours, with 1 indicating the presence and 0 the absence of the helping behaviour.

Finally, we also conducted additional analyses with a binary classification of allomaternal care provided by males (paternal care) and that provided by other group members (care by others) (data from (Isler and van Schaik, 2012; Lukas and Clutton-Brock, 2012a; Lukas and Clutton-Brock, 2013)).

Covariates

As captivity might affect body mass variation (for instance, under good husbandry conditions, most animals gain weight in captivity (Leigh, 1994)), we added provenance (wild = 1/captivity = 0) as an additional factor in all analyses. Furthermore, we analysed the subsample of studies including only wild-caught females separately.

In a previous study we found that substrate use (arboreal versus terrestrial) influenced the amount of body fat of a species (Heldstab et al., 2016). We therefore added substrate use as an additional factor in all analyses. Data from published sources were used to assign each species to one of two substrate use categories, terrestrial (0) or arboreal (1), based on their main habit. Species were classified as terrestrial when they spent more than 50% of observation time on the ground ((Meier, 1983; Gittleman, 1986; Myers et al., 2006; Rowe and Myers, 2011), see Additional file 1).

We also controlled for several other potential methodological confounds. First, some studies include body mass data from pregnant and lactating females in the population mean, which may artificially increase annual body mass variation in seasonal breeders. Pregnancy affects a female's weight due to the added weight of the offspring and the associated tissues and fluids. To control for this effect, we added the variable "inclusion of reproductive females in the study" as a covariate. Second, we added the number of months sampled as covariate. Ideally, we would have preferred to use only those studies from the wild that reported the mean body mass for 12 consecutive months. However, in contrast to studies in captivity, most body mass data of wild living mammals have been recorded less frequently. Third, to control for allometric effects of size, we performed all analyses including log-transformed mean body mass as a covariate, taking the overall mean from the same specimens for which CV body mass was determined. Finally, as variation in female body mass may be influenced by life history traits such as litter size, neonatal mass, and the duration of gestation and lactation, we also included those as potential covariates.

Statistical analyses

Statistical analyses were done in JMP™ 12.0 (SAS Institute Inc, 1989-2016) and in R3.1.3 (R Core Team, 2015). In most species that exhibit allomaternal care, various kinds of care behaviours are observed, potentially resulting in collinearity problems in the statistical analyses. We checked this by generating variance inflation factors (VIF) to assess potential multicollinearity in the full set of allomaternal care behaviours (Quinn and Keough, 2002; Dormann et al., 2013) using non-phylogenetic generalized linear models and the function "vif" ("car" package: Fox and Weisberg, 2011) in R. VIFs quantify how much the variance of an estimated model parameter is increased because of multicollinearity between predictors. The VIF for carry by the male, carry by others, provisioning by the male and provisioning by others was higher than 5, which indicates a problematic amount of covariance among predictors (Rogerson, 2001). To solve this, we summed up the frequency of occurrence of carrying by the male and by others to one single variable "carrying" and similarly provisioning by the male and provisioning by others to "provisioning". After this, the VIF of all allomaternal care behaviours in all models were less than 4, which indicates an acceptable amount of covariance among predictors (Additional file 5: Tables S1 and S2). Two life history traits (duration of gestation and neonatal mass) also showed VIFs consistently larger than 5 in all models (Additional file 5: Tables S1 and S2). To reduce the problematic multicollinearity in these models, we followed the method described in (Capellini et al., 2015): we first removed the life history variable with the highest VIF value from the models, the duration of gestation, and recalculated VIFs for the reduced models. Then, we removed neonatal mass, as it still had a VIF larger than 5. All remaining variables had VIFs lower than 5. We then repeated the analyses with the same specifications as the main analysis with these "reduced models" and assessed the relative contribution of each independent variable as described below.

We built phylogenetic generalized least-squares regressions (PGLS) models (Pagel, 1999; Freckleton et al., 2002) using the "caper" package (Orme, 2013) in R. Caper estimates PGLS model parameters in maximum likelihood (Orme, 2013) and the parameter lambda (λ), which quantifies the magnitude of the phylogenetic signal in the model residuals (Freckleton et al., 2002). The value of λ can vary between 0, indicating no phylogenetic signal, and 1, indicating that the observed pattern fits a Brownian motion model of trait evolution along the branches of the phylogeny such that similarity between species is directly proportional to relatedness (Freckleton et al., 2002). The phylogeny was based on a composite supertree from (Fritz et al., 2009) (Additional file 4: Fig. S1).

CV body mass (used as a proxy for body fat) was the dependent variable, while measures of allomaternal care and all possible confounding variables (substrate use, provenance [wild / captivity], number of months sampled, inclusion of reproductive females, mean body mass and several life history variables) were independent variables in the PGLS models. We did not log-transform CV body mass values prior to the analysis as this would not have improved the skew of its distribution. Although the predictor CV body mass was skewed towards smaller values, the distribution of the residuals of the PGLS models were normally distributed and did not comprise any outliers.

We used a model selection approach based on the AICc (Akaike Information Criterion with correction for finite sample size, Hurvich and Tsai, 1989) to determine the most important allomaternal care behaviours for female CV body mass. We ran the model selection across all possible models built with the explanatory variables mentioned above. We accounted for uncertainty in the models by performing model averaging (Grueber et al., 2011) in the candidate model set including models with $\Delta AICc < 2$ (Burnham et al., 2011). $\Delta AICc$ is the difference in AICc between the focal model and the AICc of the best-fitting model in the candidate model set. Estimates of each parameter were averaged across the candidate models (means were weighted by the Akaike weight of a given model). The relative importance of a predictor was obtained by summing the Akaike's weights of the models in the candidate model set including the focal predictor, following the method described by Symonds and Moussalli (Symonds and Moussalli, 2011). The method to perform model averaging with the PGLS function in the package "caper" (Orme, 2013) is described in (Garamszegi and Mundry, 2014) and the corresponding material is available at http://www.mpcm-evolution.org.

Results

The results confirmed our two main predictions. Model selection and averaging showed that the most important effect among allomaternal care behaviours on female CV body mass was provisioning of the young by the male and other group-members (Relative importance = 1) (Table 1, Fig. 1a). This form of allomaternal care was negatively correlated with CV body mass in reproductive females, suggesting that an energetic contribution towards offspring rearing allows females to reduce the amount of stored body fat. In contrast, allonursing, which involves no additional influx of energy but distributes maternal help across different mothers, did not correlate with CV body mass (Relative importance = 0.06) (Table 1).

Results using a binary coding scheme of allomaternal care behaviours are strikingly similar (Additional file 5: Table S6 and S8, Fig. 1b).

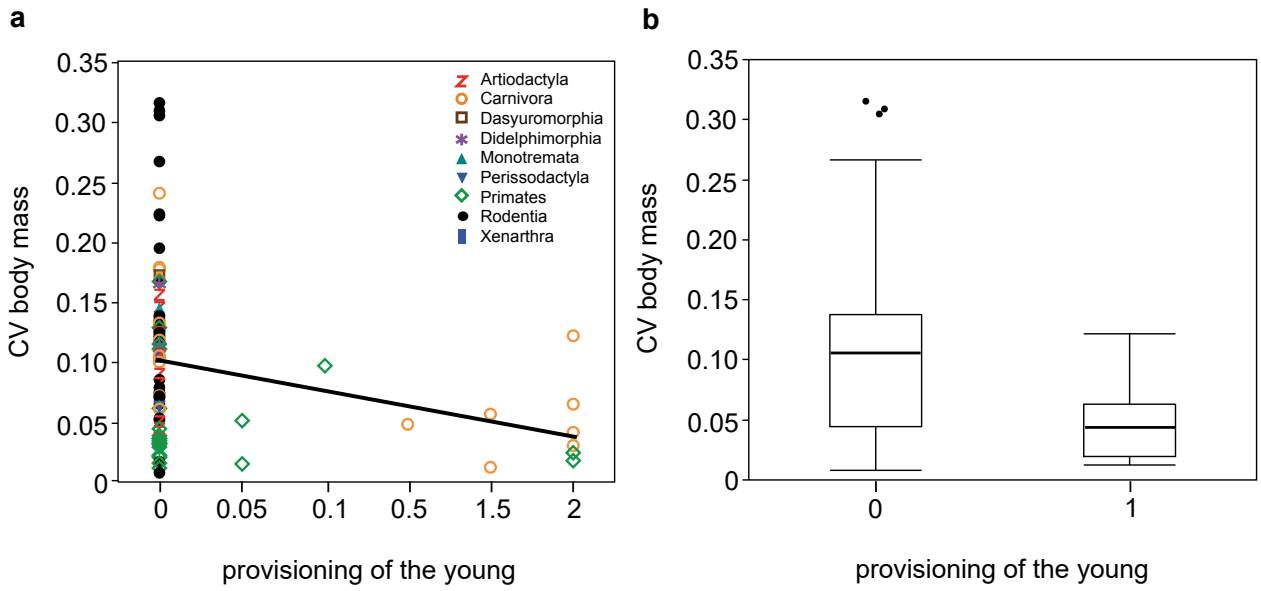

Figure 1. (**a**) Female CV body mass as a function of provisioning of the young by the male and other group members, using the continuous coding scheme. (**b**) Female CV body mass is lower in species with provisioning of the young by the male and other group members (coded as 1) than in species without it (coded as 0). Details of phylogenetic models are shown in Table 1 and Additional file 5: Table S6. Species values are listed in the Additional file 1.

Using a continuous coding scheme of paternal care and the amount of allomaternal care provided by other group members, we found that only paternal care showed a negative relationship with CV body mass (Relative importance = 1) (Table 2, Fig. 2a and b). In contrast, using a binary coding scheme, both paternal care and the amount of allomaternal care provided by other group members had a negative effect on CV body mass, although the negative effect of paternal care was stronger than that of allomaternal care by other group members (Additional file 5: Table S7 and S9, Fig. S2a and b).

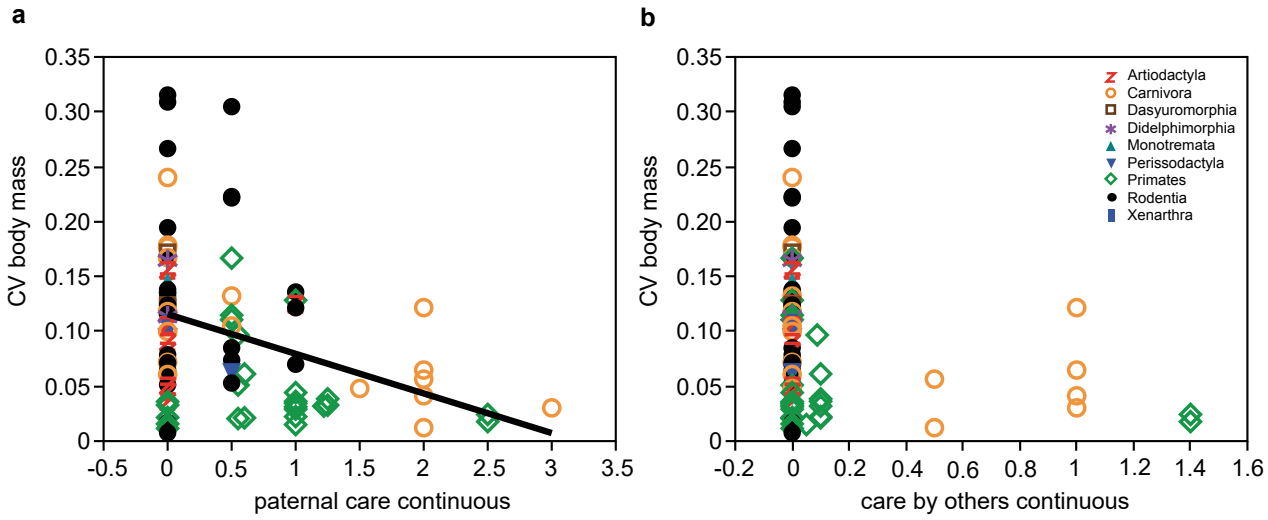

Figure 2. Female CV body mass is lower in species with paternal care (**a**) but not with care provided by other group members (**b**), using the continuous coding scheme. Details of phylogenetic models are shown in Table 2. Species values are listed in the Additional file 1.

Results for the subset of studies including only wild-caught females (*N* = 49 species) were largely similar to those obtained from the whole sample, although the effects were a bit weaker (Additional file 5: Tables S10-S15).

In all analyses substrate use and provenance were correlated with CV body mass. Arboreal species had less body fat than terrestrial and semiaquatic species, as indicated by the negative correlation between CV body mass and substrate use. Furthermore, CV body mass was higher in wild-caught specimens compared to captive ones, suggesting that wild-caught individuals experience more variation in energy intake than provisioned specimens living in captivity. Controlling for further possible confounding variables (number of months sampled, inclusion of reproductive females, mean body mass, and several life history variables) did not change the effects of the main explanatory variables. In some models, both a lower species body mass and the inclusion of reproductive females in the study were related to a lower CV body mass, while species with a relatively high reproductive rate, as indicated by larger litters, exhibited a higher CV body mass. In some models, species for which fewer months were sampled showed a larger CV body mass (Tables 1 and 2 and Additional file 5: Tables S6, S7, S12 and S13).

Table 1. Continuous classification of allomaternal care behaviours: Averaged parameter estimates and their relative explanatory importance for female CV body mass (N = 87). Gestation length and neonatal mass were excluded to reduce multicollinearity between predictors. Numbers in bold indicate predictors whose confidence intervals of their effect exclude zero.

Predictors		Relative importance of predictors	Model averaging estimates*	95% CI
intercept			0.126	**(0.100, 0.153)**
provisioning		1.00	-0.040	**(-0.043, -0.036)**
protecting		0.06	-0.001	(-0.002, 0.001)
carrying		0.07	0.003	(-0.004, 0.010)
communal nesting		0.06	0.001	(-0.002, 0.004)
allonursing		0.06	0.005	(-0.010, 0.021)
log mean body mass		0.44	-0.006	**(-0.010, -0.002)**
provenance	captive wild	0.80	na 0.025	na **(0.017, 0.032)**
substrate use	terrestrial arboreal	1.00	na -0.045	na **(-0.050, -0.041)**
number of months		0.53	-0.001	(-0.001, 0.001)
inclusion of reproductive females		0.69	-0.019	**(-0.030, -0.008)**
log litter size		0.56	0.027	**(0.013, 0.041)**
log weaning age		na	0	0

*: averaged model estimates based on 12 models with ΔAICc ($AICc_{\text{focal model}} - AICc_{\text{best model}}$) < 2 since the best AICc model is not strongly weighted (weight = 0.15) (Symonds and Moussalli, 2011). A full list of models is given in Additional file 5: Table S4. Reference levels of categorical variables have an estimate of 0; na – not applicable; 95% CI - 95% confidence interval.

Table 2. Continuous classification of paternal care and care provided by other group members: Averaged parameter estimates and their relative explanatory importance for female CV body mass (*N* = 87). Gestation length and neonatal mass were excluded to reduce multicollinearity between predictors. Numbers in bold indicate predictors whose confidence intervals of their effect exclude zero.

Predictors		Relative importance of predictors	Model averaging estimates*	95% CI
intercept			0.148	**(0.127, 0.169)**
care by others		na	0	0
paternal care		1.00	-0.028	**(-0.029, -0.027)**
log mean body mass		0.67	-0.008	**(-0.011, -0.004)**
provenance	captive wild	0.80	na 0.024	na **(0.017, 0.032)**
substrate use	terrestrial arboreal	1.00	Na -0.047	na **(-0.050, -0.043)**
number of months		0.38	-0.001	**(-0.002, -0.001)**
inclusion of reproductive females		0.37	-0.011	**(-0.020, -0.002)**
log litter size		0.24	0.007	(-0.001, 0.016)
log weaning age		na	0	0

*: averaged model estimates based on 11 models with ΔAICc ($AICc_{focal\ model} - AICc_{best\ model}$) < 2 since the best AICc model is not strongly weighted (weight = 0.15) (Symonds and Moussalli, 2011). A full list of models is given in Additional file 5: Table S5. Reference levels of categorical variables have an estimate of 0; na – not applicable; 95% CI - 95% confidence interval.

Discussion

Using annual variation in body mass, we found that this CV body mass and the amount of allomaternal care show a pattern of correlated evolution among female mammals: females of those species with more contributions of non-mothers to offspring care exhibit reduced annual variation in body mass. From this, we conclude that allomaternal energy subsidies and fat storage are compensatory strategies to stabilise the energetic costs involved in female reproduction.

First, we predicted that only an additional influx of energy in the form of costly allomaternal care behaviours by the male and other non-breeding group members towards the offspring and the mother would allow reproductive females to reduce the storage of body fat, whereas a mere redistribution of energy between mothers as in allonursing behaviour would not. As predicted, we only found a negative correlation between seasonal variation in body mass and the amount of allomaternal care in the form of provisioning of the young by the male and other group members, but not with allonursing.

This suggests that if other conspecifics take over some of the maternal costs the need for these females to store extra body fat to fuel reproduction is relaxed.

This pattern across species is consistent with numerous intraspecific studies showing that extra energy delivered by costly care behaviours of helpers allows breeding females to reduce their maternal investment. For instance, in meerkats and cooperatively breeding bird species, an increased number of helpers enabled breeding females to maintain better condition and higher body mass and achieve a higher fitness (Russell et al., 2003; Heinsohn, 2004; Charmantier et al., 2007; Klauke et al., 2013; Paquet et al., 2013). In Campbell's dwarf hamsters the presence of males protects females against extreme heat production in response to the exogenous heat requirements of the pups. As this acute increase in maternal temperature is thought to be a substantial cost to females, paternal presence likely allows females to decrease the energetic demands of reproduction (Walton and Wynne-Edwards, 1997). Another study of the same species found that removal of the male not only decreased pup survival, growth, and readiness for dispersal by 18 days of age but also resulted in an additional 20% body weight loss in the female (Mclnroy, 2000). Lastly, a comparative study across mammals reveals that male care is associated with larger litters in some species or shorter lactation time in others, resulting in increased female fecundity (West and Capellini, 2016).

Second, we investigated the effect of different types of allomaternal help (help of the male or other conspecifics) on female fat stores. Both the help provided by the breeding male and the help provided by other group members showed a negative correlation with female CV body mass. However, the relative importance of allomaternal care provided by the breeding male was greater than the relative importance of help of other caretakers. This fits well with the often-reported finding that males care unconditionally, whereas care by helpers may be more conditional (Clutton-Brock et al., 2002; Nichols et al., 2012; Marshall et al., 2016).

A broad comparative study as presented here can only provide an overview over potential patterns of correlated evolution and is limited by methodological issues. Ideally, we would have preferred to use individual variation in body fat over the year instead of the annual variation in body mass averaged over several females as used in this study. Although the published literature contains a variety of measures of adipose depots in living subjects such as palpation, skinfold thickness, perirenal adiposity, the number of adipocytes in bone marrow, and adipocyte volumes from tissue samples (Ellis, 2000), these measures have not yet been compared to each other and each measure has only been applied to very few different species making broad phylogenetic comparisons impossible.

Similarly, taking body fat values obtained from cadavers is problematic because they assess body fat at a single point in time, while the individual body fat fluctuations remain unknown [73].

It may be argued that, rather than taking annual variation in body mass, the costs of reproduction should be estimated by subtracting the maternal body weight at conception from the body weight at offspring weaning. However, such detailed data are rarely available, and may raise other issues, such as postpartum oestrus in lagomorphs, Callitrichid primates and several otariids, which means females suckle newborns while simultaneously being pregnant (Brambell, 1944; Ziegler et al., 1990; French et al., 1996; Trillmich and Wolf, 2008). Even more importantly, in most mammals such as carnivores, rodents and primates allomaternal care and its beneficial effect for mothers continues post-weaning. Thus, offspring provisioning until independence allows females to invest more time in foraging, regain body condition more quickly and mate sooner (Cantoni and Brown, 1997), which we would not capture with the body weight difference of mothers between conception and offspring weaning.

In our study, some part of the variation in female body mass may result from the increasing weight of the foetus or litter during gestation. However, without dissection this cannot be disentangled from storing energy reserves during gestation for the subsequent lactation period, which is even more energetically demanding (van Schaik and van Noordwijk, 1985). As a rough control for such effects, we included neonatal mass, litter size, gestation length and lactation time as potential correlates in the analyses, but this did not alter our findings. Moreover, because cooperative breeders tend to have higher reproductive efforts than independent breeder (Lukas and Clutton-Brock, 2012b), this possibility cannot explain the reduced CV in body mass among species receiving allomaternal care.

In our data, we found a surprisingly weak phylogenetic signal of CV body mass and thus low values of λ for the model residuals, indicating that the phylogenetic disposition for fat disposition is partially masked by habitat-caused variation (Harlow, 1995; Muehlenbein et al., 2005; Hahn, 2006). The fact that we still found significant relationships between CV body mass and allomaternal care would then make our case even stronger, because it implies that the underlying effect must be very strong.

Another unsolved question concerns the relationship between reproductive effort, seasonal fluctuations in climate or food abundance, and social factors such as allomaternal care. Reproductive seasons and experienced seasonality in food intake are generally interrelated in mammals (Bronson, 1989). There is evidence that species inhabiting more seasonal and less predictable habitats more often breed cooperatively (Clutton-Brock, 2016; Lukas and Clutton-Brock, 2017), and we also expect that they would benefit more from a higher ability to store body fat.

However, because we found a negative, rather than the expected positive correlation between allomaternal care and the tendency to store body fat, this confirms that there is indeed a trade-off due to energetic costs of fat storage, and thus that social and physiological buffers are compensatory strategies to maintain fitness in a harsh environment. To further investigate these strategies, we would not only need data on environmental factors such as annual rainfall, vegetation indices or actual food abundance, but also of the seasonality experienced by the animals themselves, as expressed in dietary habits throughout the year, analogous to our studies of brain size and seasonality in primates (van Woerden et al., 2010; van Woerden et al., 2012; van Woerden et al., 2014).

Conclusions

In conclusion, several lines of evidence suggest that any allomaternal care, be it aimed at the mother or the offspring, and be it by the father or other conspecifics, allows females to reduce the amount of stored body fat. In combination with intraspecific studies, our results further support the idea that the main reason for this negative correlation between the amount of allomaternal care and female CV body mass is the energetic contribution towards offspring rearing through costly care by males or helpers, which stabilises the energetic costs for female reproduction. Although our comparative approach has some limitations, our analyses indicate that female mammals have two different strategies of coping with energetic constraints on reproduction: either getting fat or getting help.

Declarations

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Availability of data and material

The dataset and all additional analyses supporting the conclusions of this article are available in the supplementary information files.

Authors' contributions

SAH collected the data, performed the statistical analyses and wrote the paper. CvS and KI co-wrote the manuscript. All authors contributed to the design of the study, discussed the results and gave final approval for publication.

Competing interests

The authors declare that they have no competing interests.

Consent for publication

Not applicable.

Ethics approval and consent to participate

Not applicable.

Additional files

Additional file 1: List of species and data used for this study (XLSX 22.7 kb).

Additional file 2: References for the CV body mass data used for this study (DOCX 60.7 kb).

Additional file 3: Compilation and quantification of allomaternal care behaviours (DOCX 37.3 kb).

Additional file 4: Fig. S1 Phylogenetic tree of 87 mammal species used in this study visualised using Mesquite v. 3.11 (Maddison and Maddison, 2017) (PDF 373 kb).

Additional file 5: Supplementary results: Tables S1 and S2. Results testing for collinearity among predictors. Variation inflation factors (VIF) for all the full models and all the reduced models after multicollinearity is considered. **Table S3.** We found a high estimated phylogenetic signal lambda (λ) in the individual allomaternal care variables. **Tables S4 and S5.** Model sets obtained after model selection based on ΔAICc < 2 including best-supported models and multiple-model parameter estimates. **Tables S6-S9 and Fig. S2.** Results of a binary coding scheme of allomaternal care behaviours as well as binary coded care provided by males (paternal care) or other group members (care by others). **Tables S10-S15.** Results for the subset of studies including only wild-caught females ($N = 49$). These remained largely identical to those obtained with the whole dataset (see also Tables 1 and 2 in the main text). (DOCX 169 kb)

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Additional file 1: List of species and data used for this study

group	*Genus species*	CV body mass	body mass [g]	Ref. CV body mass and body mass	allonursing	communal nesting, babysitting, retrieval	protection	provisioning by the male	provisioning by others	carry by the male
Artiodactyla	***Alces alces***	0.090	400500	Franzmann et al 1977	0	0	0	0	0	0
Artiodactyla	***Capreolus capreolus***	0.082	23808	Gehr, personal communication	0	0	0	0	0	0
Artiodactyla	***Dama dama***	0.045	34150	Weber and Thompson 1998	0	0	0	0	0	0
Artiodactyla	***Odocoileus hemionus***	0.050	54073	Jacobsen 2008	0	0	0	0	0	0
Artiodactyla	***Ovibos moschatus***	0.125	144000	Adamczewski et al 1997	0.1	0	1	0	0	0
Artiodactyla	***Potamochoerus porcus***	0.156	64120	Tierpark Hellabrunn, München, personal communication	0	0	0	0	0	0
Artiodactyla	***Rangifer tarandus***	0.145	92330	Chan-McLeod et al 1999	0	0	0	0	0	0
Artiodactyla	***Redunca fulvorufula***	0.036	28600	Skinner 1980	0	0	0	0	0	0
Artiodactyla	***Rupicapra rupicapra***	0.105	27167	Schaschl et al 2012	0	0	0	0	0	0
Carnivora	***Canis latrans***	0.122	12500	Poulle et al 1995	0.1	1	1	1	1	0
Carnivora	***Canis lupus***	0.041	28001	Seal and Mech 1983	0.1	1	1	1	1	0
Carnivora	***Halichoerus grypus***	0.179	159400	Beck et al 2003	0	0	0	0	0	0
Carnivora	***Lycaon pictus***	0.030	19568	Visee 2001	0.25	1	1	1	1	0
Carnivora	***Meles meles***	0.132	11221	Page et al 1994	0	1	0.5	0	0	0
Carnivora	***Mephitis mephitis***	0.240	2151	Verts 1967	0	0	0	0	0	0
Carnivora	***Mustela putorius***	0.061	689	Korhonen and Harri 1986	0	0	0	0	0	0
Carnivora	***Neovison vison***	0.072	692	Dunstone 1993	0	0	0	0	0	0
Carnivora	***Otaria flavescens***	0.105	120690	Tierpark Hellabrunn, München, personal communication	0	0	0.5	0	0	0
Carnivora	***Procyon lotor***	0.177	4189	Moore and Kennedy 1985	0	0	0	0	0	0
Carnivora	***Spilogale putorius***	0.100	502	Crabb 1944	0	0	0	0	0	0
Carnivora	***Urocyon cinereoargenteus***	0.048	3541	Sullivan 1956	0	0	1	0.5	0	0
Carnivora	***Ursus thibetanus***	0.118	87500	Hashimoto and Yasutake 1999	0	0	0	0	0	0
Carnivora	***Vulpes lagopus***	0.065	3019	Prestrud and Nilssen 1992	0.1	1	1	1	1	0
Carnivora	***Vulpes macrotis***	0.012	2110	Warrick and Cypher 1999	0.1	1	1	1	0.5	0
Carnivora	***Vulpes vulpes***	0.056	5620	Fairley 1970	0.1	1	1	1	0.5	0

group	*Genus species*	CV body mass	body mass [g]	Ref. CV body mass and body mass	allonursing	communal nesting, babysitting, retrieval	protection	provisioning by the male	provisioning by others	carry by the male
Carnivora	***Zalophus californianus***	0.167	86792	Tierpark Hellabrunn, München, personal communication	0	0	0	0	0	0
Dasyuromorphia	***Antechinus stuartii***	0.172	19	Banks and Dickman 2000	0	0	0	0	0	0
Dasyuromorphia	***Sminthopsis crassicaudata***	0.124	13	Morton 1978	0	0	0	0	0	0
Didelphimorphia	***Caluromys philander***	0.106	292	Julien-Laferrière, personal communication	0	0	0	0	0	0
Didelphimorphia	***Didelphis marsupialis***	0.165	1040	Julien-Laferrière, personal communication	0	0	0	0	0	0
Didelphimorphia	***Philander opossum***	0.113	444	Julien-Laferrière, personal communication	0	0	0	0	0	0
Monotremata	***Tachyglossus aculeatus***	0.144	3800	Nicol and Andersen 2007	0	0	0	0	0	0
Perissodactyla	***Equus caballus***	0.062	250000	Scheibe and Streich 2003	0.05	0	0.5	0	0	0
Primates	***Callithrix jacchus***	0.018	409	Primate station Univeristy of Zurich, personal communication	0	1	1	1	1	1
Primates	***Cheirogaleus medius***	0.128	172	Mueller 1999	0	0.5	1	0	0	0
Primates	***Daubentonia madagascariensis***	0.012	2651	Zehr et al 2014	0	0	0	0	0	0
Primates	***Eulemur coronatus***	0.029	1582	Zehr et al 2014	0	0	1	0	0	0
Primates	***Eulemur fulvus***	0.044	2392	Zehr et al 2014	0	0	1	0	0	0
Primates	***Eulemur macaco***	0.031	2501	Zehr et al 2014	0	0	1	0	0	0
Primates	***Eulemur mongoz***	0.032	1615	Zehr et al 2014	0	1	1	0	0	0.22
Primates	***Eulemur rubriventer***	0.038	2340	Zehr et al 2014	0	1	1	0	0	0.25
Primates	***Eulemur rufus***	0.034	2247	Zehr et al 2014	0	0	1	0	0	0
Primates	***Galago moholi***	0.036	158	Zehr et al 2014	0	0.5	0	0	0	0
Primates	***Hapalemur griseus***	0.033	1025	Zehr et al 2014	0	1	1	0	0	0.25
Primates	***Lemur catta***	0.022	2401	Zehr et al 2014	0.1	1	1	0	0	0
Primates	***Leontopithecus rosalia***	0.024	598	Dietz et al 1994	0	1	1	1	1	0.5
Primates	***Loris tardigradus***	0.015	173	Zehr et al 2014	0	0.5	1	0	0.05	0
Primates	***Macaca fuscata***	0.167	7750	Muroyama et al 2006	0	0.5	0.5	0	0	0
Primates	***Microcebus murinus***	0.111	84	Zehr et al 2014	0.1	0.5	0.5	0	0	0
Primates	***Microcebus rufus***	0.115	44	Randrianambinina et al 2003	0	0.5	0.5	0	0	0
Primates	***Mirza coquereli***	0.016	313	Zehr et al 2014	0	0	0	0	0	0

group	*Genus species*	CV body mass	body mass [g]	Ref. CV body mass and body mass	allonursing	communal nesting, babysitting, retrieval	protection	provisioning by the male	provisioning by others	carry by the male
Primates	***Nycticebus coucang***	0.021	1196	Zehr et al 2014	0	0	0.5	0	0	0
Primates	***Nycticebus pygmaeus***	0.033	496	Zehr et al 2014	0	0	0	0	0	0
Primates	***Otolemur garnettii***	0.022	978	Zehr et al 2014	0	0.1	0	0	0	0
Primates	***Pan troglodytes***	0.097	35200	Uehara and Nishida 1987	0	0.5	0.5	0.05	0.05	0.038
Primates	***Perodicticus potto***	0.051	824	Zehr et al 2014	0	0.5	0.5	0.05	0	0
Primates	***Propithecus coquereli***	0.021	4154	Zehr et al 2014	0	0.5	0.5	0	0	0.1
Primates	***Propithecus verreauxi***	0.061	3202	Lewis and Kappeler 2005	0	0.5	0.5	0	0	1
Primates	***Varecia variegata***	0.036	3527	Zehr et al 2014	0.1	1	1	0	0	0
Rodentia	***Acomys cahirinus***	0.194	39	Khokhlova et al 2001	0	0	0	0	0	0
Rodentia	***Acomys subspinosus***	0.168	17	Fleming and Nicolson 2002, 2003	0	1	0	0	0	0
Rodentia	***Akodon azarae***	0.309	16	Del Valle and Busch 2003	0	0	0	0	0	0
Rodentia	***Ctenomys talarum***	0.065	31	Del Valle et al 2006	0	0	0	0	0	0
Rodentia	***Cynomys ludovicianus***	0.222	776	Tileston and Lechtleitner 1966	0.1	0.5	0.5	0	0	0
Rodentia	***Erethizon dorsatum***	0.124	7114	Sweitzer and Berger 1993	0	0	0	0	0	0
Rodentia	***Marmota flaviventris***	0.074	4357	Zatzman et al 1984	0.1	0.5	0.5	0	0	0
Rodentia	***Marmota monax***	0.134	3485	Concannon et al 2001	0	0	0	0	0	0
Rodentia	***Meriones crassus***	0.125	69	Khokhlova et al 2001	0	0	0	0	0	0
Rodentia	***Meriones unguiculatus***	0.121	51	Zhang and Wang 2007	0	1	1	0	0	0
Rodentia	***Microtus californicus***	0.085	44	Batzli and Pitelka 1971	0	1	0.5	0	0	0
Rodentia	***Microtus ochrogaster***	0.136	42	Voltura 1997	0	1	1	0	0	0
Rodentia	***Microtus pennsylvanicus***	0.305	42	Iverson and Turner 1974	0	1	0.5	0	0	0
Rodentia	***Microtus pinetorum***	0.070	21	Lochmiller et al 1983	0	1	1	0	0	0
Rodentia	***Myodes rutilus***	0.315	21	Zuercher et al 1999	0	0	0	0	0	0
Rodentia	***Oryzomys palustris***	0.079	37	Cameron and Spencer 1983	0	0	0	0	0	0
Rodentia	***Reithrodontomys fulvescens***	0.074	11	Cameron and Spencer 1983	0	0	0	0	0	0
Rodentia	***Sciurus carolinensis***	0.071	433	Short and Duke 1971	0	0	0	0	0	0
Rodentia	***Sciurus niger***	0.051	742	Short and Duke 1971	0	0	0	0	0	0
Rodentia	***Sciurus vulgaris***	0.008	303	Lurz and Lloyd 2000	0	0	0	0	0	0

group	*Genus species*	CV body mass	body mass [g]	Ref. CV body mass and body mass	allonursing	communal nesting, babysitting, retrieval	protection	provisioning by the male	provisioning by others	carry by the male
Rodentia	***Sigmodon hispidus***	0.128	80	Cameron and Spencer 1983	0.1	0	0	0	0	0
Rodentia	***Spermophilus franklinii***	0.267	351	Choromanski-Norris et al 1986	0	0	0	0	0	0
Rodentia	***Spermophilus lateralis***	0.116	212	Blake 1972	0	0	0	0	0	0
Rodentia	***Spermophilus parryii***	0.223	804	Buck and Barnes 1999	0	0	0.5	0	0	0
Rodentia	***Spermophilus richardsonii***	0.053	358	Michener 1978	0	0	0.5	0	0	0
Rodentia	***Tamiasciurus hudsonicus***	0.017	230	Koprowski 2005	0	0	0	0	0	0
Rodentia	***Zapus hudsonius***	0.138	18	Morrison and Ryser 1962	0	0	0	0	0	0
Xenarthra	***Bradypus variegatus***	0.106	4670	Silva et al 2014	0	0	0	0	0	0

group	*Genus species*	carry by others	care by others continuous	care by others binary	paternal care continuous	paternal care binary	substrate use	provenance	inclusion of reproductive females	number of months
Artiodactyla	***Alces alces***	0	0	0	0	0	0	1	0	12
Artiodactyla	***Capreolus capreolus***	0	0	0	0	0	0	1	0	5
Artiodactyla	***Dama dama***	0	0	0	0	0	0	0	1	12
Artiodactyla	***Odocoileus hemionus***	0	0	0	0	0	0	0	0	11
Artiodactyla	***Ovibos moschatus***	0	0	0	1	0	0	1	0	7
Artiodactyla	***Potamochoerus porcus***	0	0	0	0	0	0	0	0	5
Artiodactyla	***Rangifer tarandus***	0	0	0	0	0	0	1	0	4
Artiodactyla	***Redunca fulvorufula***	0	0	0	0	0	0	1	0	4
Artiodactyla	***Rupicapra rupicapra***	0	0	0	0	0	0	1	0	11
Carnivora	***Canis latrans***	0	1	1	2	1	0	1	0	4
Carnivora	***Canis lupus***	0	1	1	2	1	0	0	0	12
Carnivora	***Halichoerus grypus***	0	0	0	0	0	0	1	0	5
Carnivora	***Lycaon pictus***	0	1	1	3	1	0	0	0	4
Carnivora	***Meles meles***	0	0	0	0.5	0	0	1	0	12
Carnivora	***Mephitis mephitis***	0	0	0	0	0	0	1	0	11

group	*Genus species*	carry by others	care by others continuous	care by others binary	paternal care continuous	paternal care binary	substrate use	provenance	inclusion of reproductive females	number of months
Carnivora	***Mustela putorius***	0	0	0	0	0	0	0	0	12
Carnivora	***Neovison vison***	0	0	0	0	0	0	1	0	9
Carnivora	***Otaria flavescens***	0	0	0	0.5	0	0	0	0	6
Carnivora	***Procyon lotor***	0	0	0	0	0	0	1	0	9
Carnivora	***Spilogale putorius***	0	0	0	0	0	0	1	0	10
Carnivora	***Urocyon cinereoargenteus***	0	0	0	1.5	1	0	1	0	4
Carnivora	***Ursus thibetanus***	0	0	0	0	0	0	0	0	8
Carnivora	***Vulpes lagopus***	0	1	1	2	1	0	1	0	4
Carnivora	***Vulpes macrotis***	0	0.5	1	2	0	0	1	0	4
Carnivora	***Vulpes vulpes***	0	0.5	1	2	1	0	1	0	10
Carnivora	***Zalophus californianus***	0	0	0	0	0	0	0	0	5
Dasyuromorphia	***Antechinus stuartii***	0	0	0	0	0	0	1	0	4
Dasyuromorphia	***Sminthopsis crassicaudata***	0	0	0	0	0	0	0	0	12
Didelphimorphia	***Caluromys philander***	0	0	0	0	0	1	1	0	12
Didelphimorphia	***Didelphis marsupialis***	0	0	0	0	0	1	1	0	12
Didelphimorphia	***Philander opossum***	0	0	0	0	0	0	1	0	11
Monotremata	***Tachyglossus aculeatus***	0	0	0	0	0	0	1	0	11
Perissodactyla	***Equus caballus***	0	0	0	0.5	0	0	0	0	6
Primates	***Callithrix jacchus***	0.4	1.4	1	2.5	1	1	0	1	12
Primates	***Cheirogaleus medius***	0	0	0	1	0	1	0	1	7
Primates	***Daubentonia madagascariensis***	0	0	0	0	0	1	0	1	12
Primates	***Eulemur coronatus***	0	0	0	1	0	1	0	1	12
Primates	***Eulemur fulvus***	0	0	0	1	0	1	0	1	12
Primates	***Eulemur macaco***	0	0	0	1	0	1	0	1	12
Primates	***Eulemur mongoz***	0.1	0.1	1	1.22	0	1	0	1	12
Primates	***Eulemur rubriventer***	0.1	0.1	1	1.25	0	1	0	1	12
Primates	***Eulemur rufus***	0	0	0	1	0	1	0	1	12
Primates	***Galago moholi***	0	0	0	0	0	1	0	1	12

group	*Genus species*	carry by others	care by others continuous	care by others binary	paternal care continuous	paternal care binary	substrate use	provenance	inclusion of reproductive females	number of months
Primates	***Hapalemur griseus***	0	0	0	1.25	1	1	0	1	12
Primates	***Lemur catta***	0.1	0.1	1	1	0	1	0	1	12
Primates	***Leontopithecus rosalia***	0.4	1.4	1	2.5	1	1	1	0	12
Primates	***Loris tardigradus***	0	0.05	1	1	0	1	0	1	12
Primates	***Macaca fuscata***	0	0	0	0.5	0	0	1	0	12
Primates	***Microcebus murinus***	0	0	0	0.5	0	1	0	1	12
Primates	***Microcebus rufus***	0	0	0	0.5	0	1	1	0	7
Primates	***Mirza coquereli***	0	0	0	0	0	1	0	1	12
Primates	***Nycticebus coucang***	0	0	0	0.55	0	1	0	1	12
Primates	***Nycticebus pygmaeus***	0	0	0	0	0	1	0	1	12
Primates	***Otolemur garnettii***	0	0	0	0	0	1	0	1	12
Primates	***Pan troglodytes***	1	0.088	1	0.55	0	0	1	0	9
Primates	***Perodicticus potto***	0	0	0	0.55	0	1	0	1	12
Primates	***Propithecus coquereli***	0.1	0.1	1	0.6	0	1	0	1	12
Primates	***Propithecus verreauxi***	0.1	0.1	1	0.6	0	1	1	0	7
Primates	***Varecia variegata***	0.1	0.1	1	1	0	1	0	1	12
Rodentia	***Acomys cahirinus***	0	0	0	0	0	0	1	1	4
Rodentia	***Acomys subspinosus***	0	0	0	0	0	0	1	0	7
Rodentia	***Akodon azarae***	0	0	0	0	0	0	1	0	4
Rodentia	***Ctenomys talarum***	0	0	0	0	0	0	1	0	4
Rodentia	***Cynomys ludovicianus***	0	0	0	0.5	0	0	1	0	11
Rodentia	***Erethizon dorsatum***	0	0	0	0	0	1	1	0	7
Rodentia	***Marmota flaviventris***	0	0	0	0.5	0	0	0	0	6
Rodentia	***Marmota monax***	0	0	0	0	0	0	0	0	12
Rodentia	***Meriones crassus***	0	0	0	0	0	0	1	1	4
Rodentia	***Meriones unguiculatus***	0	0	0	1	0	0	1	1	4
Rodentia	***Microtus californicus***	0	0	0	0.5	0	0	1	1	12
Rodentia	***Microtus ochrogaster***	0	0	0	1	1	0	1	1	4

group	*Genus species*	carry by others	care by others continuous	care by others binary	paternal care continuous	paternal care binary	substrate use	provenance	inclusion of reproductive females	number of months
Rodentia	***Microtus pennsylvanicus***	0	0	0	0.5	0	0	1	0	12
Rodentia	***Microtus pinetorum***	0	0	0	1	0	0	1	0	6
Rodentia	***Myodes rutilus***	0	0	0	0	0	0	1	0	4
Rodentia	***Oryzomys palustris***	0	0	0	0	0	0	1	0	12
Rodentia	***Reithrodontomys fulvescens***	0	0	0	0	0	0	1	0	12
Rodentia	***Sciurus carolinensis***	0	0	0	0	0	1	0	1	12
Rodentia	***Sciurus niger***	0	0	0	0	0	1	0	1	12
Rodentia	***Sciurus vulgaris***	0	0	0	0	0	1	1	1	4
Rodentia	***Sigmodon hispidus***	0	0	0	0	1	0	1	0	12
Rodentia	***Spermophilus franklinii***	0	0	0	0	0	0	1	0	4
Rodentia	***Spermophilus lateralis***	0	0	0	0	0	0	0	0	12
Rodentia	***Spermophilus parryii***	0	0	0	0.5	0	0	1	0	6
Rodentia	***Spermophilus richardsonii***	0	0	0	0.5	0	0	1	0	6
Rodentia	***Tamiasciurus hudsonicus***	0	0	0	0	0	1	1	0	12
Rodentia	***Zapus hudsonius***	0	0	0	0	0	0	0	0	4
Xenarthra	***Bradypus variegatus***	0	0	0	0	0	1	1	0	11

group	*Genus species*	litter size	neonatal mass	gestation length	lactation time
Artiodactyla	***Alces alces***	1.25	13000	231	150
Artiodactyla	***Capreolus capreolus***	1.76	1210	165	94
Artiodactyla	***Dama dama***	1.00	4690	233	147
Artiodactyla	***Odocoileus hemionus***	1.64	3010	204	120
Artiodactyla	***Ovibos moschatus***	1.00	10500	257	254
Artiodactyla	***Potamochoerus porcus***	3.50	750	120	92
Artiodactyla	***Rangifer tarandus***	1.00	5510	228	183
Artiodactyla	***Redunca fulvorufula***	1.19	2720	223	82
Artiodactyla	***Rupicapra rupicapra***	1.00	2250	122	113
Carnivora	***Canis latrans***	5.69	200	62	42
Carnivora	***Canis lupus***	4.97	474	63	63
Carnivora	***Halichoerus grypus***	1.00	14000	240	19
Carnivora	***Lycaon pictus***	7.10	298	72	56
Carnivora	***Meles meles***	2.99	90	49	92
Carnivora	***Mephitis mephitis***	5.69	33	68	56
Carnivora	***Mustela putorius***	8.48	10	35	50
Carnivora	***Neovison vison***	4.76	9	31	42
Carnivora	***Otaria flavescens***	1.00	12800	312	366
Carnivora	***Procyon lotor***	3.04	83	63	112
Carnivora	***Spilogale putorius***	5.07	12	50	54
Carnivora	***Urocyon cinereoargenteus***	3.79	104	57	84
Carnivora	***Ursus thibetanus***	2.00	366	200	82
Carnivora	***Vulpes lagopus***	7.29	69	53	63
Carnivora	***Vulpes macrotis***	4.49	40	51	46
Carnivora	***Vulpes vulpes***	4.59	101	52	49
Carnivora	***Zalophus californianus***	1.00	6340	240	345
Dasyuromorphia	***Antechinus stuartii***	6.80	0	28	91
Dasyuromorphia	***Sminthopsis crassicaudata***	7.14	0	16	65
Didelphimorphia	***Caluromys philander***	4.16	0	24	120
Didelphimorphia	***Didelphis marsupialis***	6.84	0	14	100
Didelphimorphia	***Philander opossum***	4.75	0	14	80
Monotremata	***Tachyglossus aculeatus***	1.00	0	34	175
Perissodactyla	***Equus caballus***	1.00	37900	337	210
Primates	***Callithrix jacchus***	2.14	28	144	77
Primates	***Cheirogaleus medius***	2.04	15	62	45
Primates	***Daubentonia madagascariensis***	1.00	122	166	198
Primates	***Eulemur coronatus***	1.53	58	125	168
Primates	***Eulemur fulvus***	1.01	75	121	183
Primates	***Eulemur macaco***	1.00	61	126	135
Primates	***Eulemur mongoz***	1.00	60	129	150
Primates	***Eulemur rubriventer***	1.00	85	123	135
Primates	***Eulemur rufus***	1.00	75	120	183
Primates	***Galago moholi***	1.60	12	124	84
Primates	***Hapalemur griseus***	1.02	45	138	121

group	*Genus species*	litter size	neonatal mass	gestation length	lactation time
Primates	***Lemur catta***	1.17	76	136	179
Primates	***Leontopithecus rosalia***	2.00	52	125	91
Primates	***Loris tardigradus***	1.00	11	171	135
Primates	***Macaca fuscata***	1.01	502	175	195
Primates	***Microcebus murinus***	2.00	5	60	40
Primates	***Microcebus rufus***	2.52	7	60	40
Primates	***Mirza coquereli***	1.70	18	86	86
Primates	***Nycticebus coucang***	1.00	51	193	180
Primates	***Nycticebus pygmaeus***	1.75	20	185	133
Primates	***Otolemur garnettii***	1.76	52	132	140
Primates	***Pan troglodytes***	1.02	1750	235	1460
Primates	***Perodicticus potto***	1.00	37	197	212
Primates	***Propithecus coquereli***	1.00	100	162	168
Primates	***Propithecus verreauxi***	1.00	103	159	183
Primates	***Varecia variegata***	2.04	94	102	146
Rodentia	***Acomys cahirinus***	2.43	5	38	28
Rodentia	***Acomys subspinosus***	2.37	6	38	28
Rodentia	***Akodon azarae***	4.59	2	23	14
Rodentia	***Ctenomys talarum***	4.39	8	103	35
Rodentia	***Cynomys ludovicianus***	4.45	15	35	41
Rodentia	***Erethizon dorsatum***	1.00	491	211	56
Rodentia	***Marmota flaviventris***	4.65	34	31	25
Rodentia	***Marmota monax***	4.10	27	32	44
Rodentia	***Meriones crassus***	4.40	3	26	20
Rodentia	***Meriones unguiculatus***	5.00	3	25	26
Rodentia	***Microtus californicus***	4.29	3	21	16
Rodentia	***Microtus ochrogaster***	3.78	3	23	21
Rodentia	***Microtus pennsylvanicus***	5.17	2	21	14
Rodentia	***Microtus pinetorum***	2.43	2	21	21
Rodentia	***Myodes rutilus***	5.61	2	24	334
Rodentia	***Oryzomys palustris***	4.33	4	25	11
Rodentia	***Reithrodontomys fulvescens***	3.77	1	20	14
Rodentia	***Sciurus carolinensis***	2.91	15	44	65
Rodentia	***Sciurus niger***	2.71	15	45	75
Rodentia	***Sciurus vulgaris***	3.99	9	39	70
Rodentia	***Sigmodon hispidus***	5.30	7	27	15
Rodentia	***Spermophilus franklinii***	9.14	9	28	42
Rodentia	***Spermophilus lateralis***	5.02	6	27	32
Rodentia	***Spermophilus parryii***	6.49	11	25	28
Rodentia	***Spermophilus richardsonii***	7.49	6	23	29
Rodentia	***Tamiasciurus hudsonicus***	4.08	7	34	56
Rodentia	***Zapus hudsonius***	5.53	1	19	28
Xenarthra	***Bradypus variegatus***	0.92	272	171	26

Additional file 2: References for the CV body mass data used for this study

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Additional file 3: Compilation and quantification of allomaternal care behaviours

Data for this study was retrieved from (Isler and van Schaik, 2012) and supplemented with additional data for 30 species collected in the same manner. Data on allomaternal care behaviours were compiled and quantified as follows:

Values on allomaternal care behaviour were compiled from published compilations (Spencer-Booth, 1971; Gubernick, 1981; Emlen, 1984; Dewsbury, 1985; Whitten, 1987; Bronson, 1989; Packer et al., 1992; Gittleman, 1994; Woodroffe and Vincent, 1994; Snowdon, 1996; Solomon and French, 1997; Hayes, 2000; Ross and MacLarnon, 2000; König, 2006; Silk, 2007; Wilson and Mittermeier, 2009), the Mammalian Species accounts (1969-2014), reliable online sources (Animal Diversity Web (Myers et al., 2006), and All the World's Primates (Rowe and Myers, 2011) and original sources for individual species (see also (Isler and van Schaik, 2012))).

Allomaternal care behaviour was divided into the following categories: carrying, provisioning, allonursing, protection, thermoregulation/babysitting and pup retrieval and coded as follows:

Provisioning by the male/provisioning by others: This refers to the frequency of provisioning by the male/by other group members. It was set to 1, if the male/other group members usually actively shared or provisioned food, to 0.75 if passive sharing was more frequent (70-80%) but active sharing was common (20-30%), to 0.5 if passive sharing was common and active sharing rare, to 0.1 if passive sharing was rare, and to 0.05 if single observations of food sharing or provisioning were reported.

Carrying by the male/carry by others: This refers to the frequency of carrying by the male/by other group members. If the offspring was carried 50% of the time, the value was 0.5. When carrying behaviour was limited to pup retrieval it was counted in the category of thermoregulation, babysitting and pup retrieval below.

Protection: This refers to the occurrence of active protection by the male, defence of territory, or defence against predators. It was considered absent if territories were only protected against other males, and females or young may even be hurt during agonistic encounters between males. Otherwise, we scored protection as 1 if it was usual, 0.5 if frequent, 0.1 if rare, and 0.05 if single observations were reported. If more precise values were given in the original sources, those were used.

Thermoregulation, babysitting and pup retrieval: This refers to the occurrence of babysitting during the mother's absence, retrieving pups, or carrying offspring to a new nest, by the male or other group members, huddling, and communal nesting during the breeding period. It was scored as follows: 1 if it was usual, 0.5 if frequent, 0.1 if rare, and 0.05 if single observations were reported. If more precise values were given in the original sources, those were used.

Allonursing: This refers to the frequency of allonursing of an infant. The values given by (Packer et al., 1992) were converted as follows: (<10%) was set to 0.1, 10-45% (less than own mother) to 0.25, and as much as own mother to 0.5. If more precise values were given in the original source, these were used.

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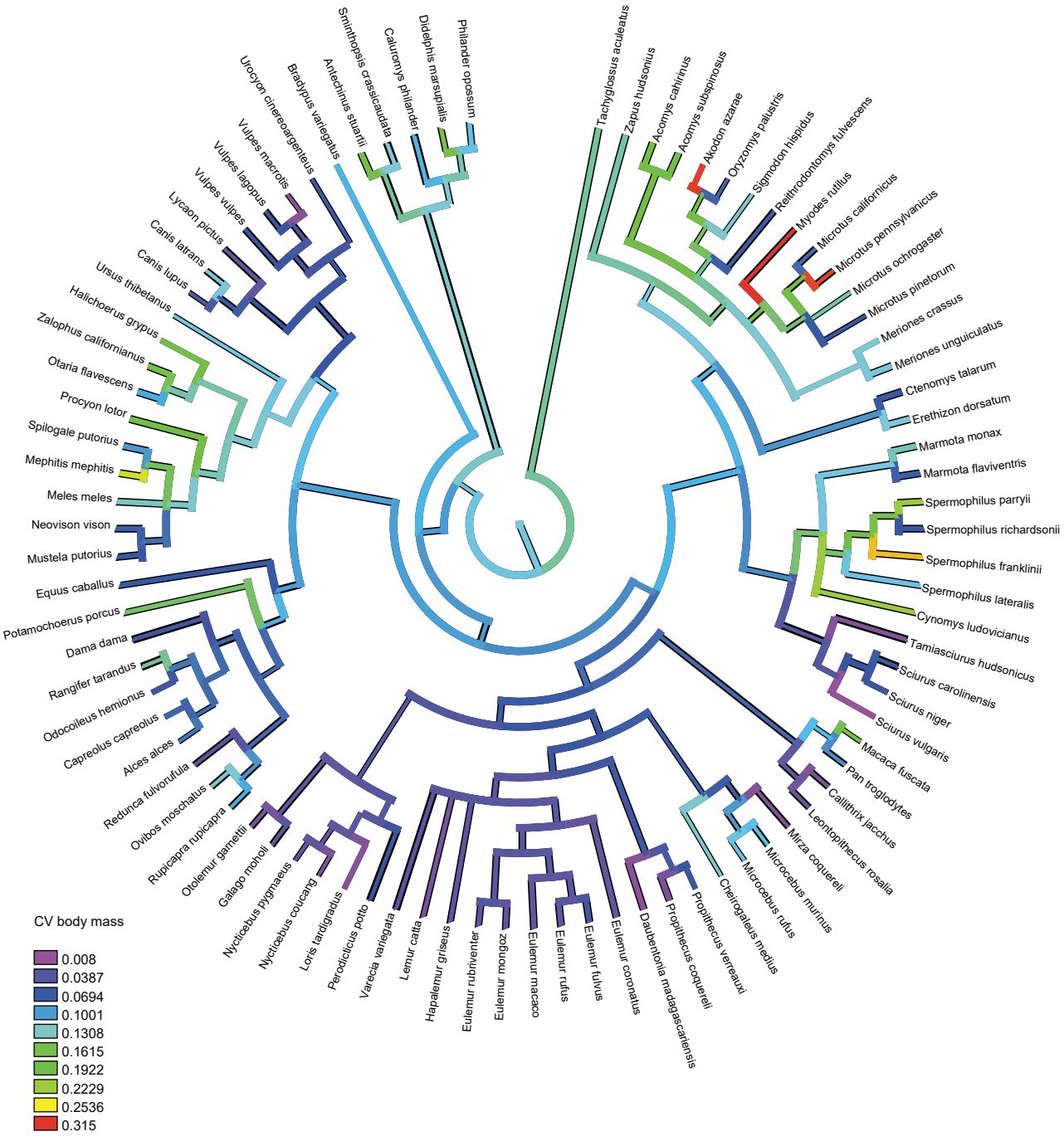
Additional file 4: Figure S1. Phylogenetic tree of 87 mammal species used in this study visualised using Mesquite v. 3.11 (Maddison and Maddison, 2017)



Additional file 5: Supplementary results

Results testing for collinearity among predictors

Table S1. Variance inflation factors (VIF) of the predictor variables for female CV body mass in the full models and the reduced models, when all allomaternal care behaviours are entered separately as predictors. Values of VIF greater than 5 indicate a problematic amount of covariance among predictors (Rogerson, 2001). For the reduced models "na" indicate that a given predictor variable has been excluded from the models due to its high VIF value in the full model.

	continuous classification of allomaternal care behaviours		**binary classification of allomaternal care behaviours**	
VIF for predictor variables:	**full model**	**reduced model**	**full model**	**reduced model**
provisioning	2.98	2.81	1.71	1.57
protecting	2.30	2.28	2.03	1.99
carrying	1.98	1.96	1.68	1.67
comm. nesting, babysit, retrieval	2.63	2.59	2.59	2.59
allonursing	1.97	1.96	1.60	1.59
log mean body mass	6.99	2.98	6.85	2.80
provenance	1.96	1.86	1.92	1.79
substrate use	2.93	2.68	2.79	2.47
number of months sampled	1.64	1.49	1.60	1.45
incl. of reproductive females	2.91	2.87	2.70	2.64
log litter size	5.96	3.08	5.32	2.66
log weaning age	2.57	2.08	2.71	2.24
log gestation length	10.82	na	10.71	na
log neonatal mass	10.51	na	10.61	na

Table S2. Variance inflation factors (VIF) of the predictor variables for female CV body mass in the full models and the reduced models, when paternal care and care provided by other group members are entered as predictor variables. Values of VIF greater than 5 indicate a problematic amount of covariance among predictors (Rogerson, 2001). For the reduced models "na" indicate that a given predictor variable has been excluded from the models due to its high VIF value in the full model.

	continuous classification of paternal care and care by others		**binary classification of paternal care and care by others**	
VIF for predictor variables:	**full model**	**reduced model**	**full model**	**reduced model**
care by others	3.59	3.21	1.93	1.93
paternal care	3.29	3.12	1.98	1.92
log mean body mass	6.50	2.47	6.50	2.43
provenance	1.86	1.74	1.86	2.32
substrate use	2.70	2.42	2.62	2.32
number of months sampled	1.59	1.42	1.59	1.44
incl. of reproductive females	2.62	2.57	2.55	2.48
log litter size	5.46	2.63	4.96	2.57
log weaning age	2.49	1.96	2.47	1.98
log gestation length	10.85	na	9.97	na
log neonatal mass	10.43	na	10.29	na

Estimated phylogenetic signal (λ) in the individual allomaternal care variables

Table S3. The estimated phylogenetic signal (λ) in the individual variables using the "est.lambda()" function in the "caper" package (Orme, 2013) in R was high for the individual allomaternal care variables and very low for CV body mass.

	λ for continuous predictor variables	**λ for binary predictor variables**
provisioning	0.938	1.000
protecting	0.913	0.774
carrying	1.000	0.848
communal nesting, babysit, retrieval	0.640	0.643
allonursing	0.444	0.507
paternal care	0.948	0.716
care by others	0.889	0.779

Model sets obtained after model selection based on ΔAICc < 2

Table S4. Continuous classification of allomaternal care behaviours: Model set obtained after model selection based on ΔAICc < 2 for all reduced models where gestation length and neonatal mass have been excluded to reduce multicollinearity. Best-supported models and multiple-model parameter estimates for the relationship between female CV body mass and allomaternal care behaviours. For the averaged parameter estimates and their relative explanatory importance see Table 1 in the main text.

explanatory variables													model information					
(Intercept)	provisioning	protecting	carrying	communal nesting	allonursing	log mean body mass	provenance	substrate use	number of months sampled	incl. of reproductive females	log litter size	log weaning age	lambda	df	log likelihood	AICc	Δ AICc	weight
0.08	-0.04	-	-	-	-	-	0.04	-0.05	-	-	0.05	-	0	5	130.63	-248.21	0.00	0.15
0.16	-0.03	-	-	-	-	-0.01	0.02	-0.05	-	-0.03	-	-	0	6	131.52	-247.63	0.58	0.11
0.18	-0.03	-	-	-	-	-0.02	-	-0.05	-	-0.05	-	-	0	5	130.24	-247.43	0.78	0.10
0.21	-0.04	-	-	-	-	-0.01	-	-0.04	-0.01	-0.05	-	-	0	6	131.40	-247.37	0.83	0.10
0.09	-0.04	-	-	-	-	-	0.03	-0.04	-	-0.02	0.05	-	0	6	131.39	-247.36	0.85	0.10
0.10	-0.04	-	-	-	-	-	0.03	-0.04	-0.01	-	0.05	-	0	6	131.13	-246.83	1.37	0.08
0.18	-0.04	-	-	-	-	-0.01	0.02	-0.04	-0.01	-0.03	-	-	0	7	132.23	-246.61	1.60	0.07
0.08	-0.05	-	0.04	-	-	-	0.04	-0.05	-	-	0.05	-	0	6	131.00	-246.58	1.63	0.07
0.14	-0.03	-	-	-	-	-0.01	0.04	-0.06	-	-	-	-	0	5	129.78	-246.52	1.69	0.06
0.09	-0.04	-0.01	-	-	-	-	0.04	-0.05	-	-	0.05	-	0	6	130.87	-246.32	1.89	0.06
0.08	-0.05	-	-	-	0.10	-	0.04	-0.05	-	-	0.05	-	0	6	130.84	-246.27	1.94	0.06
0.09	-0.05	-	-	0.02	-	-	0.03	-0.03	-	-0.03	0.05	-	0	7	132.03	-246.22	1.99	0.06

- for absence of the predictor in the model; "df", degree of freedom; "log Likelihood"; log likelihood of the model; "AIC_c", Akaike's information criterion corrected for sample size; "ΔAIC_c", difference in AIC_c between the focal model and the model with the lowest AIC_c; "weight", relative probability of a model within the full set of models.

Table S5. Continuous classification of paternal care and care provided by other group members: Model set obtained after model selection based on ΔAICc < 2 for all reduced models where gestation length and neonatal mass have been excluded to reduce multicollinearity. Best-supported models and multiple-model parameter estimates for the relationship between female CV body mass and paternal care and care by others. For the averaged parameter estimates and their relative explanatory importance see Table 2 in the main text.

explanatory variables										model information					
(Intercept)	care by others	paternal care	log mean body mass	provenance	substrate use	number of months sampled	incl. of reproductive females	log litter size	log weaning age	lambda	df	log likelihood	AICc	Δ AICc	weight
0.14	-	-0.03	-0.01	0.03	-0.06	-	-	-	-	0	5	130.06	-247.06	0.00	0.15
0.10	-	-0.03	-	0.03	-0.04	-	-	0.04	-	0	5	129.79	-246.52	0.54	0.11
0.16	-	-0.03	-0.01	0.02	-0.05	-	-0.02	-	-	0	6	131.90	-246.39	0.67	0.11
0.21	-	-0.03	-0.01	-	-0.04	-0.01	-0.03	-	-	0	6	130.86	-246.29	0.77	0.10
0.19	-	-0.03	-0.01	-	-0.05	-	-0.04	-	-	0	5	129.60	-246.15	0.91	0.10
0.11	-	-0.03	-	0.04	-0.05	-	-	-	-	0	4	128.40	-246.06	1.01	0.09
0.16	-	-0.03	-0.01	0.03	-0.05	-0.01	-	-	-	0	6	130.73	-246.03	1.03	0.09
0.18	-	-0.03	-0.01	0.02	-0.04	-0.01	-0.02	-	-	0	7	131.69	-245.53	1.53	0.07
0.12	-	-0.03	-	0.03	-0.04	-0.01	-	0.03	-	0	6	130.43	-245.43	1.63	0.07
0.13	-	-0.03	-0.01	0.03	-0.05	-	-	0.02	-	0	6	130.31	-245.20	1.86	0.06
0.13	-	-0.03	-	0.03	-0.04	-0.01	-	-	-	0	5	129.06	-245.07	1.99	0.06

- for absence of the predictor in the model; "df", degree of freedom; "log Likelihood"; log likelihood of the model; "AIC_c", Akaike's information criterion corrected for sample size; "ΔAIC_c", difference in AIC_c between the focal model and the model with the lowest AIC_c; "weight", relative probability of a model within the full set of models.

Results of a binary coding scheme of allomaternal care behaviours as well as binary coded care provided by males (paternal care) or other group members (care by others)

Table S6. Binary classification of allomaternal care behaviours: Averaged parameter estimates and their relative explanatory importance for female CV body mass (N = 87). Gestation length and neonatal mass are excluded to reduce multicollinearity between predictors.

predictors		**Relative importance of predictors**	**Model averaging estimates***	**95% CI**
intercept			0.151	**(0.130, 0.172)**
provisioning		1.00	-0.060	**(-0.062, -0.058)**
protecting		na	0	0
carrying		na	0	0
communal nesting		0.16	0.002	(-0.001, 0.006)
allonursing		na	0	0
log mean body mass		0.78	-0.010	**(-0.013, -0.007)**
provenance	captive wild	0.70	na 0.021	na **(0.013, 0.030)**
substrate use	terrestrial arboreal	1.00	na -0.049	na **(-0.052, -0.045)**
number of months		0.27	-0.001	**(-0.001, -0.001)**
incl. of reproductive females		0.68	-0.024	**(-0.035, -0.014)**
log litter size		0.15	0.005	(-0.002, 0.013)
log weaning age		0.06	0.001	(-0.002, 0.004)

*: averaged model estimates based on 13 models with ΔAICc ($AICc_{\text{focal model}} - AICc_{\text{best model}}$) < 2 since the best AICc model is not strongly weighted (weight = 0.13) (Symonds and Moussalli, 2011). A full list of models is given in Table S8. Reference levels of categorical variables have an estimate of 0; na – not applicable; 95% CI - 95% confidence interval, the 95% confidence intervals that do not overlap zero are presented in bold.

Table S7. Binary classification of paternal care and care provided by other group members: Averaged parameter estimates and their relative explanatory importance for female CV body mass (N = 87). Gestation length and neonatal mass are excluded to reduce multicollinearity between predictors.

predictors		Relative importance of predictors	Model averaging estimates*	95% CI
intercept			0.155	**(0.138, 0.173)**
care by others		0.35	-0.014	**(-0.026, -0.002)**
paternal care		0.76	-0.035	**(-0.046, -0.023)**
log mean body mass		0.91	-0.012	**(-0.014, -0.010)**
provenance	captive	0.80	na	na
	wild		0.025	**(0.018, 0.032)**
substrate use	terrestrial	1.00	na	na
	arboreal		-0.055	**(-0.058, -0.051)**
number of months		0.27	-0.001	(-0.001, 0.001)
incl. of reproductive females		0.48	-0.015	**(-0.024, -0.006)**
log litter size		0.15	0.005	(-0.001, 0.012)
log weaning age		na	0	0

*: averaged model estimates based on 14 models with ΔAICc ($AICc_{focal\ model} - AICc_{best\ model}$) < 2 since the best AICc model is not strongly weighted (weight = 0.13) (Symonds and Moussalli, 2011). A full list of models is given in Table S9. Reference levels of categorical variables have an estimate of 0; na – not applicable; 95% CI - 95% confidence interval, the 95% confidence intervals that do not overlap zero are presented in bold.

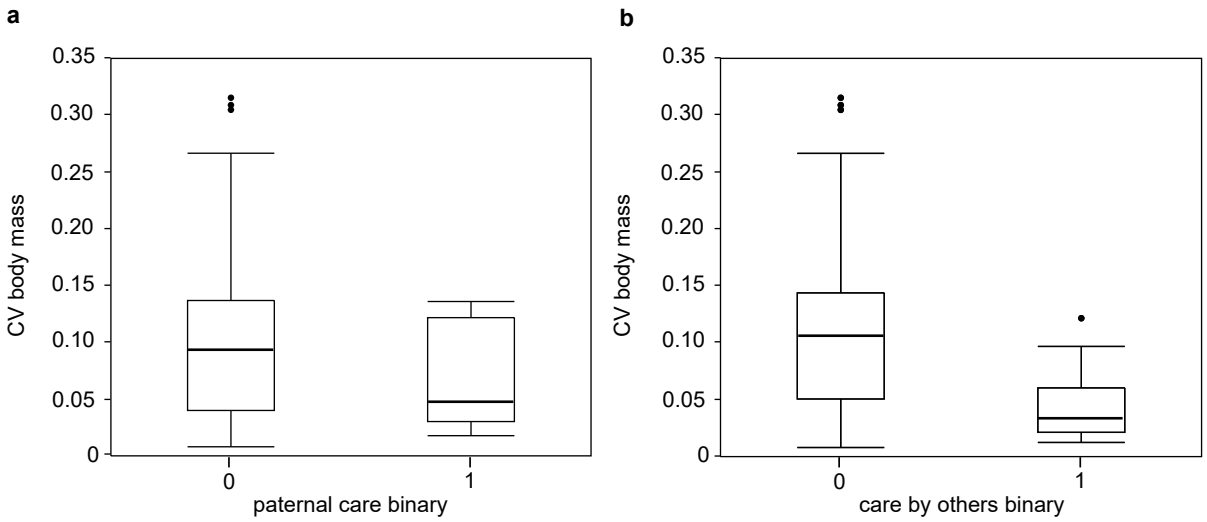


Figure S2. Female CV body mass is lower in species with paternal care (**a**) and with care provided by other group members (**b**) with the binary coding scheme. Details of phylogenetic models are shown in Table S7. Species values are listed in the Additional file 1.

Table S8. Binary classification of allomaternal care behaviours: Model set obtained after model selection based on ΔAICc < 2 for all reduced models where gestation length and neonatal mass have been excluded to reduce multicollinearity. Best-supported models and multiple-model parameter estimates for the relationship between female CV body mass and allomaternal care behaviours. For the averaged parameter estimates and their relative explanatory importance see Table S6.

explanatory variables													model information					
(Intercept)	provisioning	protecting	carrying	communal nesting	allonursing	log mean body mass	provenance	substrate use	number of months sampled	incl. of reproductive females	log litter size	log weaning age	lambda	df	log likelihood	AICc	Δ AICc	weight
0.16	-0.06	-	-	-	-	-0.01	0.02	-0.05	-	-0.03	-	-	0	6	132.02	-248.62	0.00	0.13
0.14	-0.06	-	-	-	-	-0.01	0.04	-0.06	-	-	-	-	0	5	130.57	-248.09	0.52	0.10
0.18	-0.06	-	-	-	-	-0.01	-	-0.05	-	-0.04	-	-	0	5	130.56	-248.07	0.54	0.10
0.09	-0.06	-	-	-	-	-	0.04	-0.05	-	-	0.04	-	0	5	130.53	-248.00	0.61	0.10
0.21	-0.06	-	-	-	-	-0.01	-	-0.04	-0.01	-0.04	-	-	0	6	131.65	-247.88	0.74	0.10
0.18	-0.06	-	-	-	-	-0.01	0.02	-0.04	-0.01	-0.03	0.05	-	0	8	132.65	-247.45	1.17	0.07
0.10	-0.06	-	-	-	-	-	0.04	-0.06	-	-	-	-	0	4	129.04	-247.34	1.28	0.07
0.13	-0.06	-	-	-	-	-0.02	0.03	-0.05	-	-0.03	0.05	0.02	0	8	132.49	-247.13	1.49	0.06
0.15	-0.07	-	-	0.01	-	-0.01	0.02	-0.05	-	-0.03	0.05	-	0	8	132.44	-247.04	1.58	0.06
0.18	-0.07	-	-	0.01	-	-0.01	-	-0.05	-	-0.05	-	-	0	6	131.11	-246.79	1.82	0.05
0.09	-0.06	-	-	-	-	-	0.03	-0.04	-	-0.02	0.03	-	0	6	131.06	-246.70	1.91	0.05
0.15	-0.06	-	-	-	-	-0.01	0.03	-0.06	-0.01	-	0.05	-	0	7	131.04	-246.67	1.95	0.05
0.20	-0.07	-	-	-0.02	-	-0.01	-	-0.04	-0.01	-0.05	-	-	0	7	132.24	-246.63	1.99	0.05

- for absence of the predictor in the model; “df”, degree of freedom; “log Likelihood”; log likelihood of the model; “AIC_c”, Akaike’s information criterion corrected for sample size; “ΔAIC_c”, difference in AIC_c between the focal model and the model with the lowest AIC_c; “weight”, relative probability of a model within the full set of models.

Table S9. Binary classification of paternal care and care provided by other group members: Model set obtained after model selection based on ΔAICc < 2 for all reduced models where gestation length and neonatal mass have been excluded to reduce multicollinearity. Best-supported models and multiple-model parameter estimates for the relationship between female CV body mass and paternal care and care by others. For the averaged parameter estimates and their relative explanatory importance see Table S7.

explanatory variables										model information					
(Intercept)	care by others	paternal care	log mean body mass	provenance	substrate use	number of months sampled	incl. of reproductive females	log litter size	log weaning age	lambda	df	log likelihood	AICc	Δ AICc	weight
0.14	-	-0.05	-0.01	0.03	-0.06	-	-	-	-	0	5	128.75	-244.44	0.00	0.13
0.16	-	-0.05	-0.01	0.03	-0.05	-	-0.03	-	-	0	6	129.85	-244.27	0.17	0.12
0.08	-	-0.06	-	0.04	-0.05	-	-	0.04	-	0	5	128.43	-243.81	0.64	0.09
0.19	-	-0.04	-0.02	-	-0.05	-	-0.04	-	-	0	5	128.39	-243.73	0.71	0.09
0.15	-0.05	-	-0.01	0.03	-0.06	-	-	-	-	0	5	128.32	-243.58	0.86	0.08
0.21	-	-0.05	-0.02	-	-0.05	-0.01	-0.04	-	-	0	6	129.24	-243.06	1.38	0.06
0.14	-0.02	-0.03	-0.01	0.03	-0.06	-	-	-	-	0	6	129.18	-242.95	1.50	0.06
0.16	-0.05	-	-0.01	0.03	-0.05	-	-0.02	-	-	0	6	129.17	-242.92	1.53	0.06
0.12	-	-0.05	-0.01	0.03	-0.06	-	-	0.02	-	0	6	129.09	-242.76	1.68	0.05
0.16	-	-0.05	-0.01	0.03	-0.06	-0.01	-	-	-	0	6	129.09	-242.76	1.69	0.05
0.18	-	-0.05	-0.01	0.02	-0.04	-0.01	-0.03	-	-	0	7	130.29	-242.74	1.70	0.05
0.17	-0.05	-	-0.01	0.03	-0.06	-0.01	-	-	-	0	6	128.97	-242.52	1.93	0.05
0.16	-0.02	-0.03	-0.01	0.03	-0.05	-	-0.03	-	-	0	7	130.16	-242.48	1.96	0.05
0.21	-0.05	-	-0.02	-	-0.05	-0.01	-0.04	-	-	0	6	128.95	-242.47	1.97	0.05

- for absence of the predictor in the model; “df”, degree of freedom; “log Likelihood”; log likelihood of the model; “AIC_c”, Akaike’s information criterion corrected for sample size; “ΔAIC_c”, difference in AIC_c between the focal model and the model with the lowest AIC_c; “weight”, relative probability of a model within the full set of models.

Results for the subset of studies including only wild-caught females

The subset of studies including only wild-caught females has been analysed using a continuous classification of care behaviours. Results using a binary coding scheme are very similar (not shown).

Table S10. Variance inflation factors (VIF) of the allomaternal care behaviours as predictor variables for female CV body mass in the full models and the reduced models, when all allomaternal care behaviours are entered separately as predictors, for the subset only including wild-caught females (N = 49). Values of VIF greater than 5 indicate a problematic amount of covariance among predictors (Rogerson, 2001). For the reduced models "na" indicate that a given predictor variable has been excluded from the models due to its high VIF value in the full model.

VIF for predictor variables:	full model	reduced model
provisioning	3.81	3.73
protecting	2.80	2.67
carrying	2.25	2.11
comm. nesting, babysit, retrieval	3.26	3.24
allonursing	1.79	1.77
log mean body mass	6.83	3.43
substrate use	1.46	1.33
number of months sampled	1.73	1.41
incl. of reproductive females	1.67	1.60
log litter size	4.36	2.68
log weaning age	2.15	1.72
log gestation length	11.59	na
log neonatal mass	10.45	na

Table S11. Variance inflation factors (VIF) of the predictor variables for female CV body mass in the full models and the reduced models, when paternal care and care provided by other group members are entered as predictor variables, for the subset only including wild-caught females (N = 49). Values of VIF greater than 5 indicate a problematic amount of covariance among predictors (Rogerson, 2001). For the reduced models "na" indicate that a given predictor variable has been excluded from the models due to its high VIF value in the full model.

	continuous classification of paternal care and care by others	
VIF for predictor variables:	**full model**	**reduced model**
care by others	3.55	3.22
paternal care	3.39	3.13
log mean body mass	5.14	2.27
substrate use	1.36	1.21
number of months sampled	1.44	1.18
incl. of reproductive females	1.39	1.30
log litter size	3.78	1.85
log weaning age	1.98	1.56
log gestation length	11.30	na
log neonatal mass	10.21	na

Table S12. Allomaternal care behaviours: Averaged parameter estimates and their relative explanatory importance for female CV body mass in a subset only including wild-caught females (N = 49).

predictors		**Relative importance of predictors**	**Model averaging estimates***	**95% CI**
intercept			0.140	**(0.124, 0.156)**
provisioning		0.85	-0.038	**(-0.048, -0.027)**
protecting		0.27	-0.011	(-0.022, 0.001)
carrying		na	0	0
communal nesting		na	0	0
allonursing		na	0	0
log mean body mass		0.21	-0.002	(-0.005, 0.001)
substrate use	terrestrial	0.85	na	na
	arboreal		-0.045	**(-0.057, -0.033)**
number of months sampled		na	0	0
incl. of reproductive females		0.26	-0.009	(-0.019, 0.001)
log litter size		0.44	0.026	**(0.008, 0.043)**
log weaning age		na	0	0

*: averaged model estimates based on 12 models with ΔAICc ($AICc_{\text{focal model}} - AICc_{\text{best model}}$) < 2 since the best AICc model is not strongly weighted (weight = 0.15) (Symonds and Moussalli, 2011). A full list of models is given in Table S14. Reference levels of categorical variables have an estimate of 0; na – not applicable; 95% CI - 95% confidence interval, the 95% confidence intervals that do not overlap zero are presented in bold.

Table S13. Paternal care and care provided by other group members: Averaged parameter estimates and their relative explanatory importance for female CV body mass in a subset only including wild-caught females (N = 49).

predictors		**Relative importance of predictors**	**Model averaging estimates***	**95% CI**
intercept			0.147	**(0.119, 0.175)**
care by others		na	0	0
paternal care		1.00	-0.038	**(-0.041, -0.036)**
log mean body mass		0.23	-0.002	(-0.007, 0.003)
substrate use	terrestrial arboreal	0.86	na -0.047	na **(-0.074, -0.020)**
number of months		na	0	0
incl. of reproductive females		na	0	0
log litter size		0.43	0.022	(-0.008, 0.052)
log weaning age		na	0	0

*: averaged model estimates based on 4 models with ΔAICc ($AICc_{\text{focal model}} - AICc_{\text{best model}}$) < 2 since the best AICc model is not strongly weighted (weight = 0.34) (Symonds and Moussalli, 2011). A full list of models is given in Table S15. Reference levels of categorical variables have an estimate of 0; na – not applicable; 95% CI - 95% confidence interval, the 95% confidence intervals that do not overlap zero are presented in bold.

Table S14. Allomaternal care behaviours: Model set obtained after model selection based on ΔAICc < 2 for all reduced models where gestation length and neonatal mass have been excluded to reduce multicollinearity. Best-supported models and multiple-model parameter estimates for the relationship between female CV body mass and allomaternal care behaviours for the subset of studies including only wild-caught females (N = 49). For the averaged parameter estimates and their relative explanatory importance see Table S12.

explanatory variables													model information					
(Intercept)	provisioning	protecting	carrying	communal nesting	allonursing	log mean body mass	provenance	substrate use	number of months sampled	incl. of reproductive females	log litter size	log weaning age	lambda	df	log likelihood	AICc	Δ AICc	weight
0.12	-0.05	-	-	-	-	-	0.03	-0.05	-	-	0.05	-	0	5	63.54	-115.68	0.00	0.15
0.14	-0.04	-	-	-	-	-	0.03	-0.05	-	-	-	-	0	4	62.26	-115.61	0.07	0.14
0.10	-0.05	-	-	-	-	-	0.04	-	-	-	0.06	-	0	4	61.87	-114.83	0.85	0.10
0.17	-0.04	-	-	-	-	-0.01	0.04	-0.05	-	-	-	-	0	5	62.97	-114.55	1.13	0.08
0.12	-0.05	-	-	-	-	-	0.04	-0.05	-	-0.04	0.06	-	0	6	64.27	-114.53	1.15	0.08
0.15	-	-0.05	-	-	-	-	-	-0.06	-	-	-	-	0	3	61.71	-114.51	1.17	0.08
0.19	-	-0.05	-	-	-	-0.01	-	-0.06	-	-	-	-	0	4	62.73	-114.06	1.62	0.07
0.15	-0.04	-	-	-	-	-	0.02	-0.05	-	-0.03	-	-	0	5	62.66	-113.93	1.75	0.06
0.15	-0.03	-0.03	-	-	-	-	0.04	-0.06	-	-	-	-	0	5	62.64	-113.89	1.79	0.06
0.19	-0.04	-	-	-	-	-0.01	0.04	-0.05	-	-0.04	-	-	0	6	63.92	-113.85	1.84	0.06
0.11	-0.05	-	-	-	-	-	0.02	-	-	-0.04	0.07	-	0	5	62.58	-113.77	1.91	0.06
0.12	-0.04	-0.02	-	-	-	-	0.03	-0.05	-	-	0.05	-	0	6	63.87	-113.74	1.94	0.06

- for absence of the predictor in the model; "df", degree of freedom; "log Likelihood"; log likelihood of the model; "AIC_c", Akaike's information criterion corrected for sample size; "ΔAIC_c", difference in AIC_c between the focal model and the model with the lowest AIC_c; "weight", relative probability of a model within the full set of models.

Table S15. Paternal care and care provided by other group members: Model set obtained after model selection based on ΔAICc < 2 for all reduced models where gestation length and neonatal mass have been excluded to reduce multicollinearity. Best-supported models and multiple-model parameter estimates for the relationship between female CV body mass and paternal care and care by others for the subset of studies including only wild-caught females (N = 49). For the averaged parameter estimates and their relative explanatory importance see Table S13.

explanatory variables										model information					
(Intercept)	care by others	paternal care	log mean body mass	provenance	substrate use	number of months sampled	incl. of reproductive females	log litter size	log weaning age	lambda	df	log likelihood	AICc	Δ AICc	weight
0.15	-	-0.04	-	0.03	-0.06	-	-	-	-	0	4	62.76	-116.60	0.00	0.34
0.13	-	-0.04	-	0.02	-0.05	-	-	0.05	-	0	5	63.83	-116.26	0.35	0.29
0.18	-	-0.04	-0.01	-	-0.06	-	-	-	-	0	4	63.59	-115.78	0.83	0.23
0.11	-	-0.04	-	0.03	-	-	-	0.06	-	0	4	61.85	-114.79	1.81	0.14

- for absence of the predictor in the model; "df", degree of freedom; "log Likelihood"; log likelihood of the model; "AIC_c", Akaike's information criterion corrected for sample size; "Δ AIC_c", difference in AIC_c between the focal model and the model with the lowest AIC_c; "weight", relative probability of a model within the full set of models.

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Orme, D., 2013. The caper package: comparative analysis of phylogenetics and evolution in R. R package version 5.

Chapter 5

General discussion

Summary, future directions and implications

The aim of this thesis was to investigate (i) which strategies different mammalian species use to buffer environmental seasonality and under which ecological conditions a particular strategy is more likely to occur, and (ii) how these different buffering strategies are connected to each other.

In chapter 2, we found a positive relationship between food manipulation complexity and brain size within primates. Furthermore, we found that manipulation complexity was particularly high in species that use cognitively challenging food acquisition techniques, such as extractive foraging and tool use. These findings are in line with the *Technical Intelligence hypothesis* and its relative, the *Extractive Foraging hypothesis* which assume that enhanced food acquisition skills such as tool use and extractive foraging selected for higher-level cognition and brain enlargement (Parker and Gibson, 1977; Byrne, 1997). Our study provides also support for the broader *Cognitive Buffer hypothesis* (Allman et al., 1993; Deaner et al., 2003; Sol, 2009) as relatively large-brained primates are able to perform more complex food manipulations allowing them to find and/or access hidden or protected high-quality food sources. Because extracted food resources are often available year-round, species able to exploit them can keep their energy intake relatively constant throughout the year and hence also buffer lean periods in seasonal habitats (van Woerden et al., 2010; 2012; van Woerden et al., 2014). Our results provide further evidence that ecological challenges such as in our study complex food handling and processing are linked to brain size evolution (Parker and Gibson, 1977; Byrne, 1997; Barton, 2012; Melin et al., 2014; Benson-Amram et al., 2016; Graber et al., in revision-a).

Despite the many palpable fitness benefits of enhanced manipulative skills mentioned above (see also Gibson, 1986), living in a complex foraging niche also involves substantial costs. Not only do large-brained species need to overcome the high energetic brain growth and maintenance costs (Mink et al., 1981; Holliday, 1986; Rolfe and Brown, 1997; Niven and Laughlin, 2008) to be able to benefit from the advantages of enhanced cognitive abilities, they will also require lengthy periods of learning complex foraging skills during which failures are common and net yields are low (2012; Schuppli et al., 2016). Our pilot study on the ontogenetic trajectory of food manipulations of 30 primate species performed during the course of this thesis, illustrates that skill competence in food manipulation is reached later in species with a more complex adult manipulation repertoire (Fig. 1a).

Our preliminary results suggest that immatures in species with a more complex manipulation repertoire do not only need to learn a larger amount of different manipulations, but also develop their skills generally more slowly (Fig. 1b). As brain is the structure that allows for learning development, it is expected to be tightly linked to learning rates. We will therefore pursue this direction of research in the future to examine whether species with slower brain growth will also be slower in the development of their manipulative skills. Not only the speed of brain growth differs between primate species (Leigh, 2004; McFarlin et al., 2013; Sakai et al., 2013), there is also much variation in the developmental status of brains at birth (percent of adult brain size at birth) (Leigh, 2004; Barton and Capellini, 2011; Capellini et al., 2011). We therefore aim to test in a future study whether species with a more developed brain learn their manipulative skill repertoire faster than species with a less developed brain at birth.

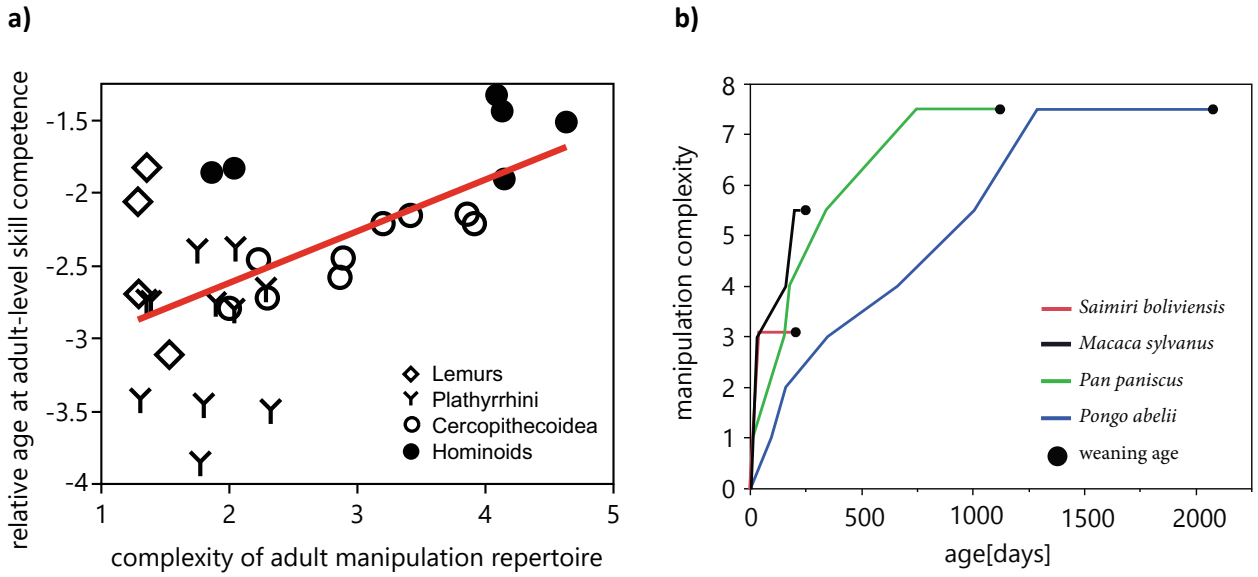

Figure 1. a) Relative age (corrected for the age of first reproduction) at adult-level manipulation skill competence as a function of the complexity of the adult manipulation repertoire (n=30, r^2_{PGLS}=0.207, p_{PGLS}=0.007). Skill competence in food manipulation is reached later in species with a more complex manipulation repertoire. **b)** Preliminary results potentially suggesting that immatures in species with a more complex manipulation repertoire develop their skills more slowly.

In chapters 3, we examined the relationship between cognitive and physiological buffering. By using a novel proxy for the tendency to store body fat – the seasonal variation of body mass within a year, measured as the coefficient of variation (CV) in body mass – we were able to test some predictions of the *Expensive Brain Framework* (Isler and van Schaik, 2009; Navarrete et al., 2011).

The *Expensive Brain Framework* postulates that the evolution of a relatively larger brain than its ancestor in a species requires that the increase in costs due to encephalization are met by some combination of the following two responses: an increase in the net energy input, or a redirection of the allocation of energy from other body functions (Fig. 2). While rejecting the validity of the *Expensive Tissue hypothesis* (Aiello and Wheeler, 1995; trade-off between the energy consumption of the digestive tract and the brain, Aiello et al., 2001)) as a general principle in mammals, Navarrete et al. (2011) found an energy trade-offs between brain size and adipose depots. Based on the *Expensive Brain Framework*, they proposed that this trade-off between fat storage and brain size is due to locomotor constraints associated with energetic costs of carrying fat depots (Fig. 2). Consistent with Navarrete et al. (2011) findings we also found a brain-fat trade-off, lending additional support to the idea that encephalization (cognitive buffering) and fat storage (physiological buffering) are compensatory strategies to buffer against seasonal food scarcity. Furthermore, in line with the predictions made by Navarrete and colleagues (2011), we found an effect of substrate use on this brain-fat trade-off, whereas a stronger trade-off was found in arboreal clades compared to terrestrial ones.

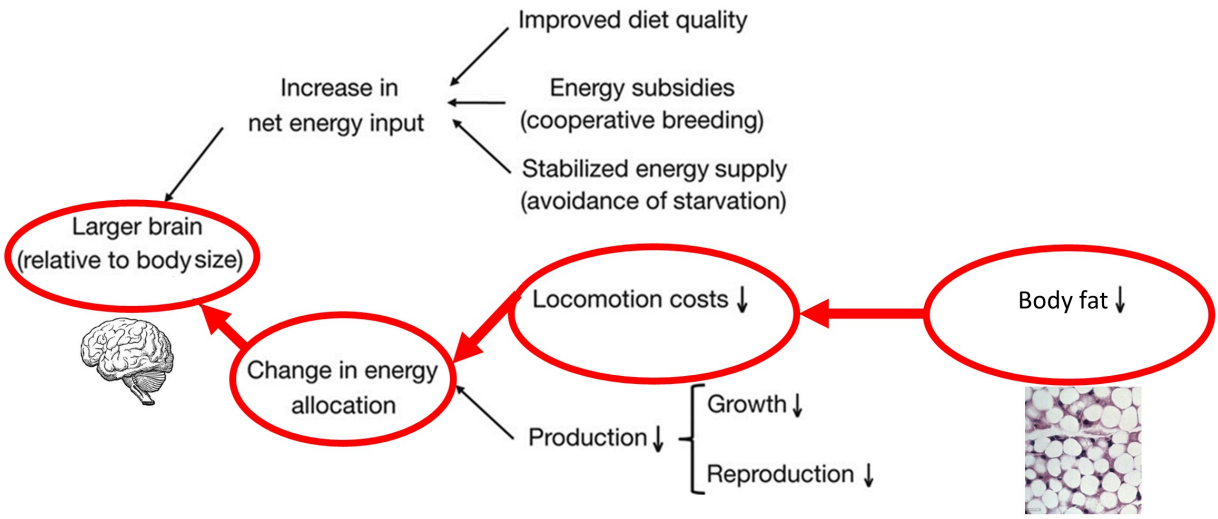

Figure 2. The findings of this thesis can be fit into the *Expensive Brain Framework* whereby a low amount of body fat reduces locomotion costs and allows redirecting this "saved" energy to the brain which, among several other factors, ultimately enabled the evolution of large brains. Also our second result that the brain-fat trade-off is stronger in arboreal species than in more terrestrial ones, as the cost of transporting additional adipose depots is higher for climbing than for horizontal locomotion fits this framework. (after Isler and van Schaik, 2009; Navarrete et al., 2011)

Our results provide the first potential explanation why cognitive buffering is more likely to occur in primates compared to other mammalian lineages. Due to the high cost of transport of additional body fat in an arboreal lifestyle involving climbing, vertical clinging and leaping (Warren and Crompton, 1998; Hanna et al., 2008), most primates may face constraints on the amount of body fat they can store, thus making most physiological buffer strategies too costly. Therefore, some primate lineages evolved another way how to survive seasonally lean periods: cognitive buffering. A recent study offers support for this claim, as Graber and colleagues (in revision-b) found no cognitive buffering in carnivores and rodents suggesting that cognitive buffering is unique to anthropoid primates, probably because the alternative, physiological buffering, might involve high fitness costs in these largely arboreal mammals.

Our hypothesis also provides an explanation for the numerous studies which showed that primates are very susceptible to obesity in captivity. For instance, 47% of the weighed captive ruffed lemurs *Varecia variegata*) were obese (Schwitzer and Kaumanns, 2001). Another study found obesity rates between 17% and 92% for nine different lemur species (Terranova and Coffman, 1997). A study in captive chimpanzees (*Pan troglodytes*) found that 11% are obese and an additional 11% are pre-obese (Videan et al., 2007). Finally, orangutans are particularly prone to become obese in captivity. A study documenting body weights of 65 orangutan females (*Pongo pygmaeus* and *P. abelii*) from various zoos found that 21 individuals were obese and 28 additional individuals were overweighed, thus together more than 75% of the whole captive sample was above the body mass range of wild orangutans (Cocks, 2007).

Besides low, respectively absent, predation risk and sometimes inappropriate diet (e.g., Oftedal and Allen, 1996; Schwitzer et al., 2009; Plowman, 2013) in a captive environment, an additional reason for the high incidence of obesity in primates might be that primates in captivity are more terrestrial compared to their counterparts in the wild. We expect an increase in body fat storage due to this “terrestriality effect” because a terrestrial lifestyle lowers the costs of transporting additional adipose tissue and predation does not counteract this effect in captivity. Assuming that this suggestion is correct, we would predict that the risk to develop obesity is strongest in species that, in the wild, are most arboreal. However, to our knowledge this hypothesis remains unexplored.

Besides body fat storage, the predominantly arboreal lifestyle of most primate species may also lead to high fitness costs for another buffering strategy, long-distance migration. Most primates are arboreal or at least semi-arboreal, making it difficult and inefficient to travel over long distances for several reasons. First, travelling modes in trees such as leaping, climbing or vertical clinging are very energy-consuming (Warren and Crompton, 1998; Hanna et al., 2008), making long-distance migration costly.

Second, for several arboreal primates plant products on trees such as leaves, fruits, seeds, gum, nectar and bark are the main food resources (Wrangham et al., 1998; Milton, 1999; Ungar and Teaford, 2002). Because storing large amounts of body fat is energetically expensive in an arboreal habitat (see section above and chapter 3) and long travels outside of forests unfeasible, arboreal primateshave to rely on having food trees available in their habitat. Third, most primates sleep in trees (Heymann, 1995; e.g., Fruth and Hohmann, 1996; Von Hippel, 1998) making long distance migrations out of habitats without trees prohibitively costly due to high predation risk on the ground (Shattuck and Williams, 2010). This is particularly true for small-bodied primates with even higher predation pressure, which sleep in tree holes or vegetation tangles (Isbell, 1994; Kappeler, 1998). Consistent with our prediction that particularly long-distance migration but also habitat switching might be a relatively inefficient way for primates to buffer seasonal food fluctuations, a comparative study across primate species found that only 10% of all 329 recorded responses to seasonality consisted of habitat shifting (Hemingway and Bynum, 2005).

Although an arboreal lifestyle has potentially negative effects on some physiological buffering strategies in primates, it is expected to have a positive effect on cognitive buffering. Large brains and enhanced cognition are able to produce a fitness benefit only if survival is sufficiently high and species are not subject to high unavoidable extrinsic mortality, such as high predation pressure (the "life-history filter", cf. van Schaik et al., 2012; Isler and van Schaik, 2014). As predation risk is lower in arboreal species compared to terrestrial ones (van Schaik et al., 1999; van Schaik and Deaner, 2003), primates are expected to have a large enough survival benefit for selection to have favoured increased brain size and hence also cognitive buffering. In summary, due to all these mentioned reasons, cognitive buffering might be particularly prevalent in the primate lineage.

As mentioned in the introduction, there are several types of physiological buffers to deal with seasonal food fluctuations. However, only body fat storage has been included in this thesis and it would evidently be very interesting to investigate how other physiological buffers such as seasonal breeding, migration or hibernation and torpor are related to cognitive buffering and hence brain size. Studies in migrating birds and bats showed that migratory species have smaller brains than sedentary species (Winkler et al., 2004; Sol et al., 2005; McGuire and Ratcliffe, 2011; Vincze, 2016). These findings raise the question whether migratory land-living mammals do also have smaller brains than sedentary species. As a study in birds (Vincze, 2016) found a negative relationship between migration distance and relative brain size, we would predict a weaker effect of migration on brain size in land-living mammals compared to bats and birds since most terrestrial mammals migrate over shorter distances than volant species (Alerstam et al., 2003). Nevertheless, as some land-living mammals migrate over several hundreds of kilometers (Teitelbaum et al., 2015), a negative correlation with brain size might still be possible.

Another physiological buffer strategy, hibernation and torpor, is also expected to show a negative correlation with brain size. We assume that selection only favours increased brain size for species which are active throughout the year and hence benefit from using their larger brains continuously, whereas species that rely mainly on body fat and reduced activity such as hibernating or torpid species are expected to exhibit relatively small brains. Furthermore, studies in European ground squirrels (*Spermophilus citellus*) showed a lower memory retention in hibernating individuals (Millesi et al., 2001) and it might be that large-brained species such as anthropoid primates which rely heavily on learnt complex skills would be too much impacted by such a memory loss. Our preliminary analysis across 1136 mammalian species indicates that there is indeed a connection between hibernation and brain size whereas hibernators do have relatively smaller brains than non-hibernating species (Fig. 3). As a next step to complement this outcome, we would like to test whether we also find a negative association between the duration of the dormant phase and relative brain size.

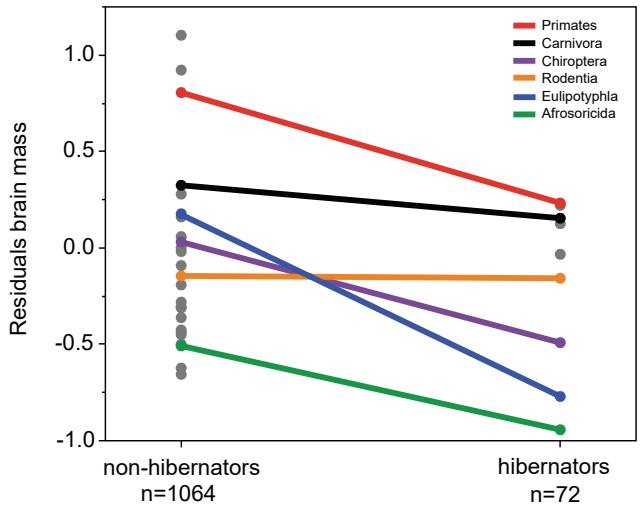

Figure 3. Relative brain size (corrected for body mass) for hibernating versus non-hibernating species (p_{PGLS}=0.002).

In chapter 3, we found a negative correlation between relative brain size and seasonal body mass variation (as a proxy for fat storage) in mammals, suggesting that cognitive buffering and physiological buffering are alternative strategies to deal with adverse energetic effects of seasonal environments. In chapter 4, we found another trade-off between two buffer strategies, physiological buffering (body fat) and care buffering (reproductive females buffer seasonality through allomaternal care by distributing the costs of reproduction over several individuals).

Our results show that both storing fat and allomaternal energy subsidies independently stabilise the energetic costs for female reproduction, but further work is needed to gain more conclusive insights whether allomaternal care including male care indeed helps to buffer seasonality as it has been shown for birds (Rubenstein and Lovette, 2007; Jetz and Rubenstein, 2011; Drobniak et al., 2015; Vincze et al., 2016).

Future work should also expand the relationship between allomaternal care and body fat to flying vertebrates, namely birds and bats. Birds show an unusually high incidence of paternal care compared to mammals. Males invest in offspring care in only about 5-10% of mammalian species (Kleiman and Malcolm, 1981; Woodroffe and Vincent, 1994), but in as many as 81% of bird species (Cockburn, 2006). The reasons for this peculiar pattern are still debated. Various authors (Ricklefs, 1968; Case, 1978; Wesolowski, 1994) have proposed that this high occurrence of paternal care in birds stems from the massive resource requirements for production of flight-capable offspring in a short period of time. Here, we propose another contributing factor for the high amounts of allomaternal care (including paternal care and cooperative breeding) in flying birds compared to terrestrial and arboreal vertebrates. Birds, at least those that fly, are expected to have higher costs of transporting adipose depots compared to terrestrial and even arboreal clades (see chapter 3). Thus, female birds may profit quite strongly from not relying on body fat as a compensatory strategy to stabilise the energetic costs for female reproduction, and thus benefiting greatly from allomaternal care. To our knowledge, a comparative study of the relationship between body fat and allomaternal care in birds has not been conducted yet. However, several experimental studies in birds showed a reduction in allomaternal care in birds which were manipulated by attaching a small weight to them suggesting also higher energetic costs of transport for additional body weight (Wright and Cuthill, 1989; Sæther et al., 1993; Schwagmeyer et al., 2002; Paredes et al., 2005). Furthermore, one study noted that artificially loaded house sparrows had a reduced ability to take-off, implying that additional load in the form of body fat might impede flight in birds (Blem, 1975), and hence that birds would profit from evolving high amounts of allomaternal care. This hypothesis predicts a strong reduction in male care and cooperative breeding in flightless birds. Testing this prediction requires targeted comparative studies.

Based on this argument, one might also expect high levels of allomaternal care in bats. Yet, in contrast to birds, the occurrence of allomaternal care is low in bats and care of offspring is mostly provided by females (although males may help guard pups or even lactate in some species (Francis et al., 1994; Kunz and Hood, 2000)). But in contrast to numerous bird species with biparental care where females lay multiple eggs, bats typically produce only single offspring. Why, then, are bats not also able to choose the alternative strategy and increase litter size through allomaternal care over evolutionary time like birds do?

There are two explanations for the apparently different constraints on reproduction in bats and birds: First, bats do not have nests and hence most young cling to their mothers (Hayssen et al., 1993; Nowak, 1994) making it virtually impossible to have more than one or two young due to space limitations. In some bat species young occasionally even cling to their mothers during flight (Davis, 1970), which might have imposed further constraints on litter size. Second, bats do have a dietary calcium limitation (Barclay, 1994, 1995; Bernard and Davison, 1996). As calcium mainly stems from the milk of the mother, it might also be a limiting factor of litter size. For these two reasons bats would profit less from allomaternal care compared to birds, which might explain why allomaternal care rarely evolved in this lineage.

The results of this dissertation have provided important insight into how mammalian species buffer seasonally lean periods. By investigating the link between brain size and manipulation complexity (cognitive buffering), allomaternal care (care buffering) and seasonal variation in body mass as a proxy for the ability to store body fat (physiological buffering), we were able to show under which ecological conditions a particular strategy is more likely to occur, and how these different buffer strategies are connected to each other. The only relationship which we did not address in this thesis so far, is the link between brain size (cognitive buffering) and allomaternal care (care buffering). The amount of energy that the mother can provide during development is thought to constrain the offspring's brain size and thus ultimately also the species' brain size (*Maternal Energy hypothesis*, Martin, 1996). Further support for this energetic-cost view provides the finding that the metabolic rate of the mother (proxied by BMR) yields an additional effect in a model predicting brain size from development periods (Martin and Isler, 2010). Because reproduction is energetically so expensive (e.g., Zenuto et al., 2002; McNab, 2006; Speakman, 2008), the *Expensive Brain Framework* postulates that one major pathway toward the evolution of larger brains was reduced allocation to reproduction (Fig. 2) (Isler and van Schaik, 2009). One way of how females achieve such a reduction in reproductive costs is by distributing these costs over other individuals such as fathers or non-breeding group members. As predicted from this perspective, a study across over 400 mammalian species found a positive correlation between brain size and the amount of help by non-mothers among mammalian clades (Isler and van Schaik, 2012). Together with the findings of this thesis, this result allows us to make the following suggestion on how the three buffering strategies how to survive seasonally lean periods are linked (Fig. 4): In chapter 3 and in the preliminary finding mentioned above that hibernating species had relatively smaller brains compared to non-hibernating species we showed that at least one form of physiological buffering, body fat storage, is negatively correlated with cognitive buffering (brain size). In chapter 4, we provide evidence that physiological buffering is negatively correlated to care buffering. It is unknown how allomaternal care is related to torpor or hibernation. In our sample of 83 hibernating species, the species of only one genus, the marmots (*Marmota),* are known to breed cooperatively (Blumstein and Armitage, 1999).

We therefore tentatively expect a negative relationship between hibernation (physiological buffering) and the amount of allomaternal care (care buffering). Lastly, the results of the previously mentioned study by Isler and van Schaik (2012) provide the missing link between the care buffering and cognitive buffering, showing that these two strategies are positively related to each other.

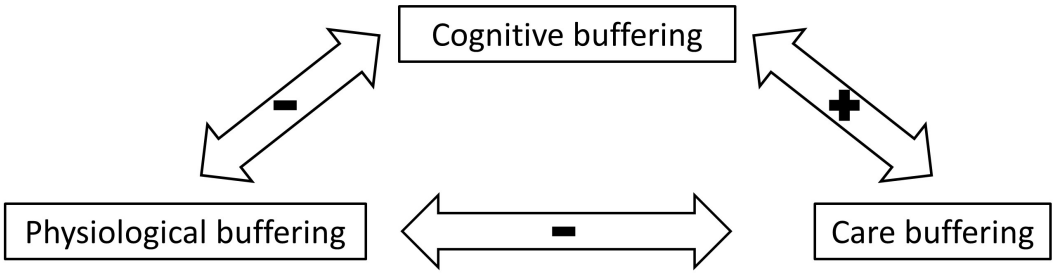

Figure 4. Suggested connections between the three different buffer strategies in mammals based on the results of this thesis and Isler and van Schaik (2012).

Seasonality and its implications for hominin evolution

One aim of this thesis is to shed light on the evolutionary history of our own species, which is characterized by an extremely large brain (Jerison, 1973; Striedter, 2005), high levels of cooperative care for offspring (Hrdy, 2009), and a relatively large amount of adipose tissue depots (Lawrence et al., 1987; Yamauchi et al., 2000; Sherry and Marlowe, 2007; Pontzer et al., 2012) compared to our closest living relatives. As an experimental approach is not feasible to understand how the abilities and peculiarities that characterize our species evolved, phylogenetic comparative analyses of a large number of mammalian species from different lineages are required. In this thesis, we provide evidence that brain size (cognitive buffer), body fat (physiological buffer), and allomaternal care (care buffer) buffer environmental seasonality in mammals. The same three buffering strategies have also been suggested to play an essential role in how human foragers cope with seasonal habitats (Kaplan et al., 2000; Wells and Stock, 2007; Wells, 2010; Smaldino et al., 2013).

In chapter 2, we show that brain size and the complexity of manipulative skills are positively correlated in primates, suggesting that large brains help to buffer seasonal fluctuations in resources by allowing to access and process alternative, often hidden and high-quality, foods. A similar argument has also been applied to human evolution. It has repeatedly been suggested that the evolution of human intelligence and hence large brain size was driven by the need to invent complex foraging techniques in an increasingly seasonal habitat (Parker and Gibson, 1977; Byrne, 1997; e.g., Antón et al., 2014). Members of the genus *Homo* did not only use tools to exploit high-quality, energy-rich food resources including difficult-to-process plant foods, such as nuts and tubers, but also hunted with weapons for meat and invented advanced technologies in food processing such as cooking (Kaplan et al., 2000; Knott, 2005; Klein, 2009; Wrangham, 2009). These techniques did further enhance improved resource quality and allowed a relatively stable energy intake all the year round as it has been shown for hunter-gatheres as models for ancestral humans (Leonard and Robertson, 1997; Kaplan et al., 2000; Berbesque et al., 2014).

An important factor for the evolution of the large human brain was the adoption of a cooperative breeding system with extensive allomaternal care (Burkart et al., 2009; Hrdy, 2009; van Schaik and Burkart, 2011). This system enabled reproductive *Homo* females to buffer seasonality by distributing the costs of reproduction over several individuals (*Care Buffer hypothesis*, see chapter 4) which allowed them to offset the costs of large brained offspring and drastically shorten their interbirth intervals as compared with great apes (Hawkes et al., 1998; Knott, 2001; Isler and van Schaik, 2012). Furthermore, the cooperative breeding system where several group members raise offspring together also increases opportunities for social learning and for extensive provisioning of the offspring (Burkart et al., 2009; van Schaik and Burkart, 2011). This allowed our ancestors to expand the period during which skills could be acquired (Gurven et al., 2006) and promoted the development of enhanced cognitive abilities (Isler and van Schaik, 2012) and ultimately the evolution into a foraging niche of unmatched complexity.

Like enhanced cognitive abilities due to a large brain, large amounts of adipose tissue are also expected to buffer seasonality in humans. Although the profile of adipose tissue through hominin evolution cannot be reliably reconstructed because of the paucity of direct fossil evidence relating to soft tissue, studies on extant apes suggest that body fat storages are a plausible adaptation to buffer seasonal variability in energy intake (Knott, 1998, 2005). Furthermore, the large seasonal body mass fluctuations in other mammals (as indicated by our CV body mass data) and the knowledge that body fat explains between 41-92% of this intraspecific body weight fluctuations provide further evidence that body fat storage is one among several other strategies how mammals and also humans buffer seasonality in energy supply (see chapter 3).

As habitat seasonality is likely to have been a key factor in the hominin radiation (Foley, 1993; Burkart et al., 2009; Wrangham, 2009), it is also plausible that energy stores may have played an essential role in early *Homo* to not only survive in these habitats but also expand their geographic range well beyond that of any other primate (Wells and Stock, 2007; Wells, 2012).

In chapter 3, we found that encephalization and fat storage are compensatory strategies to buffer against seasonal starvation and that most mammalian species follow one of these two strategies, thus resulting in a negative co-evolution between relative brain size and body fat storage. Unlike in other mammals, humans have an extremely large brain and at the same time large amounts of body fat. Furthermore, whereas mammals in general show a negative relationship between the ability to store body fat (physiological buffering) and the amount of received allomaternal care by reproductive females and their offspring (care buffering) (chapter 4), humans are also unique in this respect for a land-living mammal for combining these two strategies to buffer against resource uncertainty.

In summary, humans combine all three strategies of how to buffer seasonally lean periods which we documented among mammals: cognitive buffering by tool use and other advanced food processing technologies such as cooking, physiological buffering by storing body fat, and care buffering by intensive allomaternal care. Our results suggest that a terrestrial lifestyle with efficient bipedal walking might have been crucial to make this unique combination of all three buffer strategies possible, and so allowed our ancestors to thrive in increasingly seasonal habitats.

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Curriculum vitae

Personal information

Surname	HELDSTAB
First names	Sandra Andrea
Date of birth	30-01-1987
Nationality	Swiss
Place of origin	Saas, GR

Education

08/2013 – 06/2017	PhD thesis in Evolutionary Biology, Department of Anthropology, University of Zurich *How do mammals buffer environmental seasonality? The role of brain size, body fat and allomaternal care in dealing with energy shortage* Supervised by PD. Dr. Karin Isler and Prof. Dr. Carel van Schaik
01/2012 – 07/2013	Master of Science MNF in Biology, specialization in Behavioural Sciences, Institute of Evolutionary Biology and Environmental Studies, University of Zurich *The function of bolthole renovation in meerkats* Supervised by Prof. Dr. Marta B. Manser
09/2008 – 12/2011	Bachelor of Science MNF in Biology, University of Zurich
09/2006 – 07/2008	Bachelor in Veterinary Medicine, Vetsuisse Faculty, University of Zurich (without qualification)
08/2000 – 06/2006	Academia Engiadina (Grammar School), Samedan, Switzerland, Eidgenössische Matura (Schwerpunktfach Biologie und Chemie)

Prizes, awards, fellowships

02/2017 – 05/2017	PhD grant of the A. H. Schultz Foundation (6000 CHF)
08/2016 – 01/2017	PhD grant of the A. H. Schultz Foundation (9000 CHF)
02/2015	Student award (2nd place) for an oral talk at the GFP Conference (Gesellschaft für Primatologie) in Leipzig (D) (100 EUR)
01/2015 – 12/2015	GRC grant (Graduate Campus Grant) of the University of Zurich (9230 CHF)
09/2014	Travel grant for the EFP Conference (European Federation for Primatology) in Antwerp (B) (225 EUR)
07/2012	Travel grant of the SCNAT for the field work in South Africa for the master thesis (Swiss Academy of Sciences Foundation)(1500 CHF)

Teaching and supervision activities

07/2016 – 08/2016	Supervision – BIO555: Research internship in Anthropology
05/2016 – 06/2016	Supervison – Block course BIO211: Primate Behavior- Empirical Research
03/2016 – 03/2016	Teaching – Block course BIO209: Discovering Statistics using R
04/2015 – 04/2015	Teaching – Block course BIO209: Discovering Statistics using R
09/2014 – 10/2014	Supervison – Block course BIO210: Primate Behavior
01/2014 – 01/2014	Teaching – BIO133: Anthropologie

Institutional responsibilities

01/2015 – 12/2015	Co-organizer of the Journal Club at the Department of Anthropology, University of Zurich
01/2014 – 12/2015	Leader of the Coop-Peer-Action Group, University of Zurich
01/2013 – 07/2013	Assistance in husbandry and data collection for the meerkat colony at the Irchel campus
06/2012 – 12/2012	Field work at the Kalahari Meerkat Project, Kuruman River Reserve, Van Zylsrus, South Africa

Publications

Heldstab, S.A., Isler, K., Burkart, J.M., van Schaik, C.P. (submitted): Allomaternal care, brains and fertility in mammals: Who cares matters. *American Naturalist*

Heldstab, S.A., Müller, D.W.H., Graber, S.M., Bingaman Lackey, L., Rensch, E., Hatt, J.-M., Zerbe, P., Clauss, M. (in revision): Geographical origin, delayed implantation and induced ovulation explain reproductive seasonality in carnivores. *Journal of Biological Rhythms*

Heldstab, S.A., van Schaik, C.P., Isler, K. (in review): Getting fat or getting help? How female mammals cope with energetic constraints on reproduction. *Frontiers in Zoology* 14(1):29.

Graber, S.M., Schuppli, C., **Heldstab, S.A.**, Isler, K., van Schaik, C.P. (in revision): Ecology is the main driver of primate brain size evolution. *Evolution.*

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Oral presentations at international conferences

Heldstab, S.A. (2017). Ontogeny recapitulates phylogeny: The ontogeny of manipulation complexity within 31 primate species. 7th Congress of the European Federation for Primatology, Strasbourg, France, 21.-25.08.2017 (invited presentation).

Heldstab, S.A., Burkart, J. M., van Schaik, C.P. & Isler, K. (2017). The ontogeny of manipulation complexity within 26 primate species. AAPA 86th Annual Meeting of the American Association of Physical Anthropologists, New Orleans (L), USA, 19.-22.04.2017

Heldstab, S.A., van Schaik, C.P. & Isler, K. (2016). The Care Buffer hypothesis: reproductive females buffer seasonality through allomaternal care. 26th Congress: Joint meeting of the International Primatological Society and the American Society of Primatologists, Chicago (IL), USA, 21.-27.08.2016

Heldstab, S.A., van Schaik, C.P. & Isler, K. (2016). A fully terrestrial lifestyle allowed humans to become both fat and smart: Comparative evidence. AAPA 85th Annual Meeting of the American Association of Physical Anthropologists, Atlanta (GA), USA, 13.-16.04.2016

Heldstab, S.A., van Schaik, C.P. & Isler, K. (2015). Getting fat or getting help? How female mammals cope with energetic constraints on reproduction and brain size. 6th Congress of the European Federation for Primatology, Rome, Italy, 25.-28.08.2015

Heldstab, S.A., van Schaik, C.P. & Isler, K. (2015). Fat or smart? The role of body fat, seasonality and lifestyle in brain size evolution. CogBio conference, Zürich, Switzerland, 05.-06.03.2015

Heldstab, S.A., van Schaik, C.P. & Isler, K. (2015). Fat or smart? The role of body fat, seasonality and lifestyle in brain size evolution. GfP (Gesellschaft für Primatologie) Tagung, Leipzig, Germany, 11.-13.02.2015

Heldstab, S.A., Kosonen, Z.K., Koski, S.E., Burkart, J.M., van Schaik, C.P. & Isler, K. (2014). Manipulation complexity correlates with brain size and terrestriality across primate taxa. AAPA 83rd Annual Meeting of the American Association of Physical Anthropologists, Calgary, Canada, 08.-12.04.2014

Heldstab, S.A., Kosonen, Z.K., Koski, S.E., Burkart, J.M., van Schaik, C.P. & Isler, K. (2013). Handy hands: A comparative study of manipulation complexity across 31 species. CogBio conference, Göttingen, Germany, 02.-03.12.2013

Heldstab, S.A., Kosonen, Z.K., Koski, S.E., Burkart, J.M., van Schaik, C.P. & Isler, K. (2013). Primates manipulating the world: A comparative study of manipulation complexity across 20 species. 5th Congress of the European Federation for Primatology, Antwerp, Belgium, 10.-13.09.2013

Poster presentations at international conferences

Heldstab, S.A., Burkart, J.M., van Schaik, C.P. & Isler, K. (2017). At which age do young primates reach adult-level food manipulation competence? GfP (Gesellschaft für Primatologie) Tagung, Zürich, Switzerland, 15-17.02.2017.

van Schaik, C.P., Graber, S.M., Schuppli, C., **Heldstab, S.A.** & Isler, K. (2016). Brain size evolution in primates - testing effects of social vs. ecological complexity. 26th Congress: Joint meeting of the International Primatological Society and the American Society of Primatologists, Chicago (IL), USA, 21.-27.08.2016.

Invited Seminar Presentations

Invited seminar talk, MECADEV Meetings, CNRS, Paris (November 2016)